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THE BIOLOGY OF SOME BRITISH DELPHACIDAE (HOMOPT.) AND THEIR PARASITES WITH SPECIAL REFERENCE TO THE STREPSIPTERA

By A. I. Hassan, Ph.D., F.R.E.S.

With Thirty-two Figures.

(Read 19th October, 1938.)

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Introduction.

The Delphacidae dealt with here belong to nine species. These are: *Criomorphus williamsi* China; *Criomorphus nigrolineatus* (Scott); *Delphacodes pellucida* (Fab.); *Delphacodes difficilis* (Edw.); *Delphacodes fairmairei* (Perris); *Conomelus limbatus* (Fab.); *Stenocranus minutus* (Fab.); *Megamelus fieberi* (Scott); and *Dicranotropis hamata* (Boh.).

They are abundant in a field, known as the Willow Field, at the Imperial College Biological Field Station, Slough, Bucks. This field is covered with large clumps of grasses, rushes, and low herbaceous plants. It is surrounded with willow trees on two sides. The Delphacids live among the grasses near the ground and are gregarious. Nymphs and adults of one species, and sometimes two or three, are found in the same spot resting together on the stems of grasses and on the ground. Nymphs are found usually near the ground, and adults higher up the grass. They move sluggishly, unless disturbed, when they become active and run quickly over the stems or jump for a short distance. Some species have macropterous forms, in which the elytra are as long as, or even longer than, the abdomen. The wings of these macropterous forms help them to cover a longer distance when they jump. Edwards (1896 : 28) states that "Delphacids are for the most part small and very active insects, with plump, generally subcylindrical bodies, and frequently have the elytra not much more than half as long as the abdomen. They occur on grasses, rushes, or other low herbaceous plants, for the most part in damp places, and many are more easily obtained by searching than by sweeping."

For collecting the Delphacids, a sucking tube was found to be the best method. I started collecting the Delphacid nymphs and adults at the beginning of May 1934 and continued to collect once every two or three days until December 1934. From January 1935 until March, I collected once every month, and from April onwards collected once every three or four days. The aim of collecting at the beginning was to find the different species of Delphacids in the field and determine their life-cycles during the year. The nymphs and adults were collected from different parts of the field. On some days, only stylopised specimens were preserved as material to work on. From the beginning of the summer 1935 onwards, I collected many of the Delphacids for half an hour at different dates from different spots of the field to obtain the percentage parasitism.

The insects collected were reared separately in specimen tubes, one-fifth full of wet silver sand with four pieces of grass stems planted in it. The insect was put in it and the tube was covered by a piece of muslin secured by a rubber band. I examined these tubes daily, keeping a record of the changes which happened to the insect. The pieces of grass were changed once every week.

Life History of Delphacidae.

The Delphacids studied have one generation per year. They may pass the winter as eggs, nymphs, or adults. These different modes of hibernation are shown in the nine species dealt with here. *Conomelus limbatus* (Fab.) and *Delphacodes fairmairei* (Perris) hibernate as eggs. *Criomorphus williamsi* China, *Dicranotropis hamata* (Boh.), *Delphacodes pellucida* (Fab.), and probably *Criomorphus nigrolineatus* (Scott), and *Delphacodes difficilis* (Edw.) hibernate as nymphs. *Stenocranus minutus* (Fab.) and *Megamelus fieberi* (Scott) hibernate as adults.

In the species whose adults are absent in the summer, and in those which are not abundant, the occurrence of the egg, nymphal, and adult stages in the field was clearly discontinuous. *Criomorphus williamsi* China and *Dicranotropis hamata* (Boh.) are abundant in the field and their adults are found from May to the beginning of July. Their nymphs were found all the year round except in the second half of July. The nymphs were abundant in the field till the first half of May, when I collected 27 nymphs of *Criomorphus williamsi* China, and 8 nymphs of *Dicranotropis hamata* (Boh.). In the second half of May I collected 20 nymphs of the first species and 3 nymphs of the second; in the first half of June I collected 12 nymphs of the first and 2 nymphs of the second; and in the second half of this month I collected 4 nymphs of the first and one nymph of the second. In the first half of July I collected 2 nymphs of the first and one nymph of the second; in the second half of July, although I collected four times, I did not find any nymphs of either of these species. In the first half of August I collected 2 nymphs of *Criomorphus williamsi* China and one of *Dicranotropis hamata* (Boh.). From the second half of August till May of the next year, the numbers of their nymphs collected increased considerably.

Delphacodes pellucida (Fab.) which has the same life-cycle as the two preceding species, but is not so abundant in the field, has a longer period between the disappearance and reappearance of nymphs. In July and the first half of August I did not collect any of its nymphs. In the first half of May I collected 3 nymphs, and in the second half one nymph. In the first half of June I collected none, but one nymph was collected in the second half. In July and first half of August none was found in the eleven collections made during that period. In the second half of August I collected 5 nymphs, and from then on the nymphs were found in the field in considerable numbers till the second half of May of the next year.

In *Conomelus limbatus* (Fab.) and *Delphacodes fairmairei* (Perris), the nymphal stage alone was found in the second half of May and the whole month of June. The nymphs of the second species appear earlier than those of the first, although not in large quantities. I collected one nymph of *Delphacodes fairmairei* (Perris) in the second half of April. In the first half of May I collected one nymph. The early appearance of the last species is due perhaps to the earlier growth of fresh grass, the food-plant of *Delphacodes fairmairei* (Perris). Rush, the food-plant of *Conomelus limbatus* (Fab.) develops later. In July and August adults and nymphs are found; and in September and October the adult stage is found alone in the field.

The adult stages of *Stenocranus minutus* (Fab.) and *Megamelus fieberi* (Scott) are found alone in the field from the second half of September until the first half of April of the next year. The occurrence of the nymphs in the field differs in these two species. In *Stenocranus minutus* (Fab.) the nymphs were found in the second half of June and disappeared in the second half of Sep-

tember. There were a few in the first half of that month; in the four collections I caught only two nymphs. The nymphs of *Megamelus fieberi* (Scott) were collected in the second half of August and first half of September. I collected two nymphs in the second half of August, and one nymph in the first half of September. None was found in the second half of September.

Table I shows the stages of the different species of Delphacids present in the field at the different months of the year.

The stylopid parasite *Elenchus tenuicornis* (Kirby) is included in the table to show the relation between the different stages of the species of DELPHACIDAE and those of the parasite all the year round. This is explained later in dealing with the life-history of this parasite (Part II p. 362).

The abbreviations used in Table I are :—

E eggs.
N nymphs.
A adults.
Nn Nymphs abundant at the first half of the month and scarce at the second half.
nN Nymphs scarce at the first half of the month and abundant at the second half.
Aa Adults abundant at the first half of the month and rare at the second half.
aA Adults rare at the first half of the month and abundant at the second half.
T free living Triungulinid larva of *Elenchus*.
L Larva of *Elenchus* inside body of host.
P Male puparium of *Elenchus* appears outside the body.

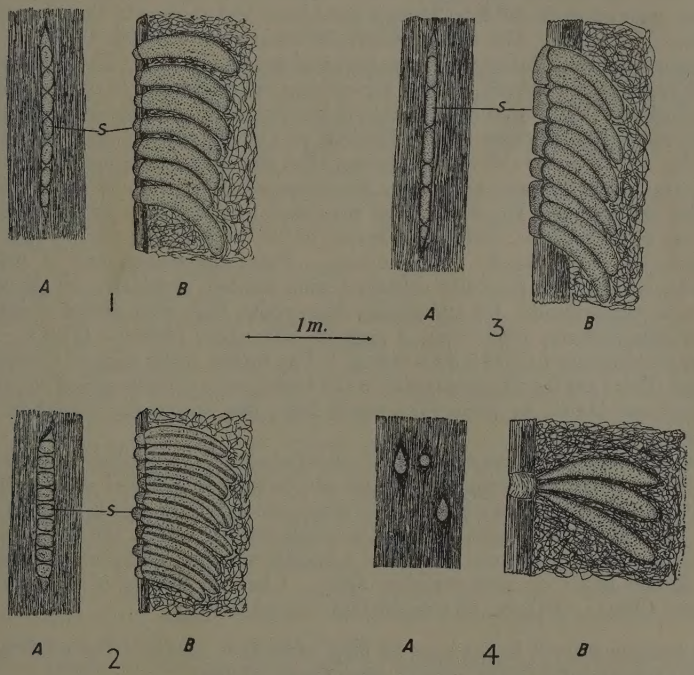
TABLE I.

Specimen	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
C. limbatus (Fab.)	E E A A	E E A A	E E A A	E E A a	E n	N N	N N a A	E N n A A	E E n A A	E E A a	E E	E E
D. fairmairei (Perris)	E E	E E	E E	E E n	E n N	N N	N n a A	E n n A A	E E A A	E E A A	E E a	E E
C. williamsi China	N N	N N	N N	N N	N N A A	E E n n A A	E E n A a	E n N	N N	N N	N N	N N
D. hamata (Boh.)	N N	N N	N N	N N a	N n A A	E E n n A A	E E n A a	E n N a	N N	N N	N N	N N
D. pellucida (Fab.)	N N	N N	N N	N N	n n A A	E E n A A	E E A a	E N	N N	N N	N N	N N
St. minutus (Fab.)	A A	A A	A A	E A a	E E	E E N	N N	N N A	n A A	A A	A A	A A
M. fieberi (Scott)	A A	A A	E A A	E E n a a	E E n N	E N N	N N	N n	n a	A A	A A	A A
E. tenuicornis (Kirby)	L L	L L	L L	L P	P A	E E A A	E T A A	L P a	E A A	E T L A A	L L	L L

Criomorphus nigrolineatus (Scott) and *Delphacodes difficilis* (Edw.) are rare, but as their nymphs were found late in summer and pass through the winter months, and their adults were found in the beginning of the summer, exactly as in *Criomorphus williamsi* China, *Dicranotropis hamata* (Boh.), and *Delphacodes pellucida* (Fab.), their life-cycles are probably the same.

A certain number of parasites were found. Eggs are parasitised occasionally by Mymarids. Nymphs are infected by Dryinids and also Stylopids.

Adults are infected by Stylopids. The Dryinids are parasitoids. When their larvae become full grown, they devour the internal viscera of the nymphs, leaving only an empty shell; after leaving the host, they spin their cocoons. Stylopids infect both nymphs and adults. If the stylopid larva is going to grow into a male, it retards the growth of the nymph, which usually grows up to the fifth instar and then dies some days after the emergence of the male Stylopid. *Conomelus limbatus* (Fab.) nymphs and probably *Delphacodes fairmairei* (Perris) nymphs hurry through their nymphal stages so quickly that the



FIGS. 1–4.—(1) Eggs of *Criomorphus williamsi* China. A. A slit in the stem of a grass showing the hardened substance (S) on the eggs. B. A section in the stem showing eggs and the hardened substance (S); (2) Eggs of *Dicranotropis hamata* (Boh.). A, B, and S, as in fig. 1; (3) Eggs of *Delphacodes fairmairei* (Perris). A, B, and S as in fig. 1; (4) Eggs of *Conomelus limbatus* (Fab.). A and B as in fig. 1.

Stylopid larvae have insufficient time for growth to a size which would affect the host and in these species, therefore, male Stylopid puparia are found in adult hosts. The parasitism by Stylopids leads to degeneration of the gonads and prevents reproduction.

The different stages in the life-cycle of the nine species of the Delphacids that are present in the field are now described.

The Egg.

Eggs of the DELPHACIDAE (figs. 1–4) are hyaline, whitish in colour, oval in shape, but slightly curved. The eggs of *Dicranotropis hamata* (Boh.) have a

white longitudinal stripe (fig. 2). In *Conomelus limbatus* (Fab.) the eggs taper towards the operculum (fig. 4). The egg is 0·8 to 1·0 mm. in length. They are laid in groups of from 3 to 24 eggs in the stems of grasses and rushes. The female holds fast to the stem of the food-plant, unsheathes her saw-like ovipositor till it becomes nearly perpendicular to her body, and pushes it into the stem, working it inwards and outwards till it forms a suitable hole in which the egg is laid. Groups of 3 to 4 eggs are laid in a single hole made in the stem of rush (fig. 4), the inner part of the egg lying in the pith. The females of the other species lay one egg in the hole, and then work downwards and lay another egg and so on till 8 to 24 eggs have been laid in the slit thus formed in the stem of grasses. The eggs regularly overlap each other in the slit. The female secretes a substance which hardens and covers the egg. These coverings appear just outside the slit. They are either oval or circular in shape. *Conomelus limbatus* (Fab.) does not secrete such substance. *Delphacodes fairmairei* (Perris) secretes a substance which hardens and blocks the slit over one or two eggs (fig. 3). Wagner (1913 : 120) states that the eggs of *Conomelus limbatus* (Fab.) are laid in the autumn; they are arranged in a group of six to twelve between the pith and the wall of the rush stem; at first the puncture in the rush was inconspicuous, but in the spring of the next year a vertical slit was visible in the wall, usually near the base. From the second half of August onwards, brown spots on stems of rushes were noticed, especially on the lower parts near the ground. On examining these spots, they were found to lead to holes containing not more than 4 eggs of *Conomelus limbatus* (Fab.). This confirms Bakkendorf (1934), who states, " The rather small eggs of *Conomelus limbatus* (Fab.) are found abundantly in the lower part of the sheath of the stem. The eggs are thrust in through a small hole, few specimens together, and arranged fan-shaped."

The slits made in grasses cannot be detected except on careful examination, when the hardened coverings of the eggs can be seen in vertical rows blocking the slit. In those species which do not hibernate as adults, egg-laying happens 28–45 days after the female attains the adult stage. When the nymphs had reached the adult stage, one female of a species was put with one male of the same species and they were watched daily. I had 56 couples of *Criomorphus williamsi* China; of these, 49 females laid eggs as follows :—

4 females started laying eggs 28 days after they attained the adult stage, 32 after about 30 days, and 13 after about 35 days.

Of 59 couples of *Conomelus limbatus* (Fab.), 43 females laid eggs as follows :—

9 females started laying eggs 29 days after they attained the adult stage, 16 after about 35 days, and 18 after about 45 days.

Of 5 couples of *Delphacodes pellucida* (Fab.), 2 females started laying eggs 30 days after they attained the adult stage, and 3 after about 33 days.

Of 11 couples of *Dicranotropis hamata* (Boh.) 4 females started laying eggs 35 days after they attained the adult stage, and 6 after about 40 days.

It may be seen from these data that the majority of the females of *Conomelus limbatus* (Fab.) require a longer period before egg-laying than those of the other three species, while the majority of the females of *Criomorphus williamsi* China require a shorter period.

In those species which hibernate as adults, the egg-laying takes place usually late in the spring. Females of *Megamelus fieberi* (Scott) were noticed

to lay eggs in February, and females of *Stenocranus minutus* (Fab.) late in April.

Conomelus limbatus (Fab.) and *Delphacodes fairmairei* (Perris) pass the winter in the egg stage.

Eggs are known to be parasitised by species of the PLATYGASTERIDAE, MYMARIDAE, ENCYRTIDAE, EULOPHIDAE, and TRICHOGRAMMATIDAE (Perkins, 1905–1906).

The only egg-parasite that I bred was a Mymarid wasp *Anagrus incarnatus* (Haliday) from the eggs of *Conomelus limbatus* (Fab.) (see p. 361).

The Nymph.

When the nymphs hatch out of the eggs, they are white in colour with red eyes and black claws. After the first ecdysis, some of them retain the white coloration and have, in addition, dark markings on the body. Others change their coloration to greyish-white, pale brown, dark brown, or black. The eyes also change their colour, usually to dark brown.

The nymphs possess most of the characters of the adult. The terminology of the different organs of the body of the adult used by Edwards (1896) is followed here.

The body of the Delphacid nymph is plump, subcylindrical, usually oval, sometimes spindle-shaped. They are small; the length varies from 0·5 to 3·6 mm. In the nymphs of the macropterous species, the vestiges of the wings are visible to the naked eye in the second instar; while in the brachypterous forms they only appear at the fourth instar. The hind tibiae of all Delphacid nymphs possess a movable toothed spur, which is characteristic of the family; and a distinctive spine on the proximal end, and another one at the centre. The antennae are of a typical homopterous type, composed of two segments. The second segment bears sensoria and a terminal seta which is usually black. Nymphs of all the species have two median facial keels all through the nymphal stage. In that respect they resemble the adults of the genus *Criomorphus*. In the adults of all the other species, the two keels become more or less fused in the adult. There are pale foveae on each side of the abdominal tergites as well as on the head. They are usually darker bordered; there is one fovea on each side of the second tergite; two foveae occur on the third and fourth; and three on the fifth to the ninth tergites.

The general coloration of the body of the nymph is variable to a certain extent. The nymphs of *C. williamsi* China vary in general coloration from light brown to black; those of *Delphacodes pellucida* (Fab.) were dull black when collected during the winter months. In captivity they became adults, which copulated and laid eggs; the eggs hatched in August to produce brownish-white nymphs. Other nymphs were collected from the field in the autumn and they were whitish-brown.

Moulting of Nymphs.

At moulting, the insect takes a firm hold of the host-plant stem by pushing its rostrum and claws into it. The nymphal skin splits along the middle line of the head and thorax on the dorsal side, and the insect emerges through the slit by peristaltic movements, releasing the head first and finishing with the abdomen. The exuviae are left attached to the stems of grasses. If it happens that the nymph falls on the ground before it has completely emerged from its skin, it is not able to finish the process of moulting and soon dies.

The degree of humidity prevailing during the process is of great importance, for if the old skin becomes too dry, the insect cannot detach itself from it; and if there is too much moisture the emerging insect cannot harden properly, and is liable to the attacks of moulds which kill it.

Food has not a great effect on the moulting periods, as grass was given to eight nymphs of *Conomelus limbatus* (Fab.) instead of rushes, their usual food. Six of them reached the adult stage after spending almost the same time in each instar as other nymphs which were fed on rushes.

Temperature has a great effect on moulting if the nymph is not hibernating. The higher the temperature, the quicker is the growth and the shorter is the stadium. Hibernating nymphs, however, appear to be unaffected by temperature. Eleven nymphs of *C. williamsi* China and *Dicranotropis hamata* (Boh.) were collected on 12 December 1934; seven of them were put at a constant temperature of 27° C. By February 1935, they were dead, without any further moulting. The other four nymphs were kept in the laboratory; one survived and commenced to moult late in March.

There are five moults, and the instars vary in duration, the last being usually the longest. In the species that hibernate as nymphs, the first three nymphal instars occur in the autumn from the middle of September to the end of October, when the nymph hibernates in the fifth instar and becomes adult in late March and April; or it occurs in the winter when the nymph hibernates as such, and the fifth instar appears late in February and in March and the adult stage is attained in late April and May.

In the laboratory, eggs of *C. williamsi* China, *D. hamata* (Boh.), and *D. pellucida* (Fab.) were laid in the summer. The pieces of grass containing the eggs were planted in tubes containing wet sand, and kept in the laboratory. In the summer of the next year, very few eggs hatched, seven eggs of *Criomorphus*, fourteen of *Dicranotropis* and four of *Delphacodes*. This suggests that these species might hibernate as eggs, but I consider these to be exceptional cases, for the following reasons :—

1. Although all the eggs were kept in the same conditions, yet only a few eggs (about 25) hatched, and the rest perished. The latter numbered more than one thousand.

2. The eggs hatched in the laboratory late in June and early in July. If such hibernated eggs were present in the field, they might be expected to hatch at that time of the year or later. The nymphs would attain a considerable size (perhaps the third instar) in a short time (as seen in Table II). In other words, the field would contain a considerable number of nymphs of the three species during the second half of July and first half of August; but as mentioned before (p. 347) no nymphs of these species were collected in the second half of July, and few only were collected in the first half of August.

3. The nymphs that hatched from these hibernated eggs reached the adult stage in about a month's time. If such eggs were found in the field, their adults would be expected in August and September but none was in fact collected (Table I).

For these reasons I do not consider that *C. williamsi* China, *D. hamata* (Boh.), and *D. pellucida* (Fab.) normally hibernate as eggs, but as nymphs. Further work on this point is necessary before definite conclusions can be reached. The eggs of these three species are not easily found in the field, and so the length of their nymphal instars obtained from the data given by the nymphs that hatched in the laboratory are included in Table II. None of the nymphs of *C. williamsi* China reached the fourth instar.

Conomelus limbatus (Fab.) and *Megamelus fieberi* (Scott) were successfully bred from the eggs. As all the nymphs that hatch do not reach the adult stage (a few of them die usually after the third and fourth moults) some incomplete data for the length of the nymphal instars have been included. In Table II, therefore, the length of each instar is based on all specimens, including those that died before becoming adult.

In *S. minutus* (Fab.) such data are recorded for all the nymphal instars except the first; as eggs never hatched in the laboratory, first instar nymphs were collected in the field.

Four nymphs of *D. difficilis* (Edw.) hatched from eggs but died before reaching the fourth and fifth instar. Eggs of *C. nigrolineatus* (Scott) were never obtained, and the nymphs collected were in an instar later than the first. This was the same with *D. fairmairei* (Perris), so these three species are not included in Table II.

Table II shows the maximum, mean, and minimum duration of each nymphal instar (except hibernating nymphs).

TABLE II.

Specimen	Length of 1st instar in days			Length of 2nd instar in days			Length of 3rd instar in days			Length of 4th instar in days			Length of 5th instar in days		
	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.
C. williamsi China	13	*9*	5	9	*5*	2	28	*14*	2	—	—	—	—	—	—
D. hamata (Boh.)	7	*6*	4	6	*5*	3	6	*4*	2	11	*6*	3	13	*10*	7
D. pellucida (Fab.)	13	*8*	3	6	*4*	3	6	*4*	2	7	*4*	2	15	*9*	4
C. limbatus (Fab.)	14	*11*	8	11	*9*	6	10	*7*	4	4	*3*	2	9	*7*	4
M. fieberi (Scott)	19	*12*	7	12	*9*	7	10	*8*	4	7	*6*	3	19	*18*	10
S. minutus (Fab.)	—	—	—	11	*9*	4	7	*4*	3	10	*8*	4	22	*18*	9

Table III shows the maximum, mean and minimum of the fourth and fifth nymphal instars of the three species that pass the winter mainly as nymphs. If the nymph hibernates at the fifth instar, the fourth instar is termed the autumn fourth instar and the fifth the winter fifth instar. On the other hand, if the nymph hibernates at the fourth instar, the fourth instar is termed the winter fourth instar, and the fifth as the spring fifth instar.

TABLE III.

Specimen	Length of autumn 4th instar in days			Length of winter 4th instar in days			Length of winter 5th instar in days			Length of spring 5th instar in days		
	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.
C. williamsi China . .	38	*31*	16	189	*159*	134	194	*185*	158	82	*47*	29
D. hamata (Boh.) . .	41	*36*	31	176	*139*	114	182	*164*	143	73	*46*	29
D. pellucida (Fab.) . .	48	*29*	8	173	*146*	127	209	*192*	162	62	*39*	31

Nymphs are known to be parasitised by Strepsiptera, DRYINIDAE, PIPUNCULIDAE, EPIPYROPIDAE, ENCYRTIDAE, and CHALCIDIDAE (Perkins, 1906).

Some of the nymphs collected were found to be parasitised by a Stylopid, by a Dryinid and by mites.

The nymphal stage is the one mainly attacked by the triungulinids of the Stylopid. As mentioned before, some species of Delphacid nymphs do not reach the adult stage if parasitised by a male Stylopid, as the adult male Stylopid reaches maturity and emerges before the nymph becomes an adult. The adult female Stylopid only appears externally in the adult Delphacids. I have never caught a Delphacid nymph in which an adult female Stylopid was visible.

Nymphs infected by a Dryinid larva do not reach the adult stage. They die when the full-grown Dryinid larva is about to leave the body, as it devours all the internal organs. In order to determine the hosts of these parasites, it was necessary to make a key for identifying the nymphs.

The following key is based on the characters of the fourth nymphal instars of the nine species of DELPHACIDAE which were available. At this instar all nymphal characters are well developed and those of the adult have not yet appeared. The description of these nymphs follows the key.

Key to the Nymphs of Nine Species of DELPHACIDAE.

1 (2). Crown longer than wide, body spindle-shaped, tapering towards both ends . . . . . *Stenocranus minutus* (Fab.).
2 (1). Crown not longer than wide.
3 (6). Crown transverse.
4 (5). Nymph brown or black with all the margins of the abdominal tergites darker in colour than their centres. . . *Criomorphus williamsi* China.
5 (4). Nymph white with black stripes, longitudinal on the thorax, and transverse on the abdomen. . . . *Criomorphus nigrolineatus* (Scott).
6 (3). Crown square.
7(10). Nymph brown, black or greyish-brown.
8 (9). Nymph of a brownish or blackish colour with pale and dark markings uniformly distributed all over the body. Median facial keels surrounded with dark colour with a small pale patch between them on the crown. . . . . *Delphacodes pellucida* (Fab.) (dark forms).
9 (8). Nymph of a uniform greyish-brown colour, on the abdomen, with whitish spots mid-way between the median line and the side of each tergite. *Conomelus limbatus* (Fab.).
10 (7). Nymph white or whitish-brown.
11(12). Nymph with a dark longitudinal stripe on each side of the body from the head to the caudal end. . . . . *Delphacodes fairmairei* (Perris).
12(11). Nymph with no dark longitudinal stripe on each side of the body; dark markings scattered uniformly over the body.
13(16). Frons with no dark markings on its lower two-thirds.
14(15). The upper third of frons dark only outside the median keels; with two short, dark, sharply defined, transverse lines on the fifth abdominal tergite near the median line. . . . . *Megamelus fieberi* (Scott).
15(14). The upper third of frons dark outside and between the median keels; with a short and a long, dark, transverse line on each side of the abdominal tergite; sometimes the colour is not sharply defined. *Dicranotropis hamata* (Boh.).
16(13). Frons with dark markings on its lower two-thirds; nymph brownish-white when alive.
17(18). Frons brownish-white with the upper third dark only outside the median keels; the lower two-thirds dark only between the median keels. . . . . *Delphacodes difficilis* (Edw.).
18(17). Frons whitish with dark longitudinal stripes between the four keels. There is also a pale patch between the median keels on the crown. *Delphacodes pellucida* (Fab.) (whitish forms).

Description of the fourth instar nymphs.

Stenocranus minutus (Fab.).

The nymph (fig. 5) is pale with a white stripe extending from the crown all along the middle portion of pro- and mesothorax. It widens on the metathorax and abdomen. About half the length of the crown projects in front of the eyes. The body is spindle-shaped, tapering towards both ends. Length 3·3–3·55 mm.

The crown is one and a half times longer than its width at the base. The two median keels are of the same colour as the crown. The basal impressions are very clear; the median line separating them is white, and forms the beginning of the white stripe mentioned above. The eyes are dark red, and the antennae pale brown.

The segments of the thorax and the crown are subequal in length. The median line is bordered with white. The side keels of pronotum are straight, reaching the hind margin. There are two black dots at the inner side of the side keels of mesothorax. These are the dorsal apodemes of the inner skeleton of the thorax seen by transparency. The part inside the keels of metathorax is white. The legs are dirty white and the tarsi are darker. Vestiges of wings appear at the second instar.

The middle part of the abdomen is white, and the lateral parts are pale brown. It is pointed at the caudal end.

Criomorphus williamsi China.

The nymph (fig. 6) is brown with pale and dark markings; sometimes pitch black with white and brown markings. The median line is white and extends from the crown all along the body to the caudal end. The two median facial keels are acute and widely separated on the whole of the frons and crown. They are pale brown bordered with dark colour. Length 2·4–2·7 mm. The nymph is peculiar in producing a noticeable amount of wax at the hind margins of the second and third abdominal segments.

The crown is wider than long. The two median keels are acute, pale in colour. The eyes are grey with the central portion dark. They are red in black specimens. The segments of the antennae are brown, edged with black.

The meso- and metathorax and crown are subequal in length. The prothorax is shorter. The median line is pale brown, bordered with white and outside this with black. The side keels of the prothorax are bent outwards, not reaching the hind margin. All the keels on the thorax are pale brown bordered with black. The legs are pale brown; the segments are dark at the joints; the last tarsal segment is dark. The legs are completely black in black specimens, and their segments are pale at the joints.

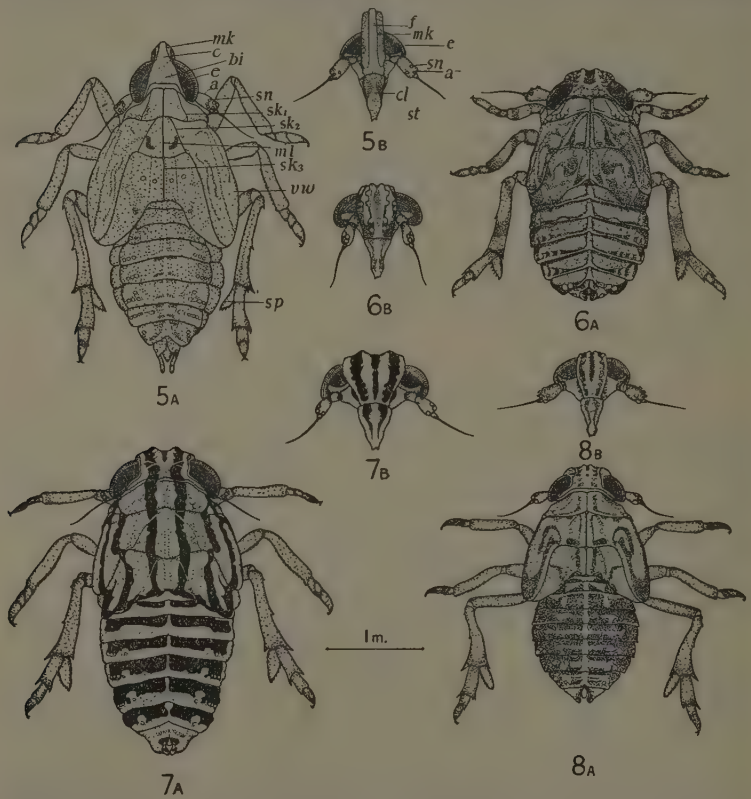
The abdomen is brown, with the edges of tergites bordered with black. The median line is white with the edges of tergites bordered with dark colour. In black specimens the pale brown and white coloration changes to brown, and the dark markings become brown. The third and fourth tergites have a wide pale patch between the median line and each lateral edge of the tergite.

Criomorphus nigrolineatus (Scott).

The nymph (fig. 7), is white with longitudinal black stripes on the crown and the thorax, and transverse ones on the abdomen. The crown has three black stripes on its anterior half; one between the two median facial keels, and one outside them on each side. It also has two black stripes on its posterior half. The prothorax has four longitudinal black stripes, the mesothorax eight, and the metathorax six. Length 3·1–3·3 mm.

The crown is wider than long; the two median keels are white and the whole area between them is black. The eyes are brown. The first segment of the antennae is white; the second is brown with dark edges.

The prothorax is a little shorter than the meso- and metathorax. These and the crown are subequal in length. The side keels of prothorax are bent outwards and do not reach the hind margin. The legs are yellowish-white, and the joints are bordered with black. The fore and middle tarsi are black, the hind tarsi have only their third segment black.



FIGS. 5a–8b.—(5a) A Nymph of *Stenocranus minutus* (Fab.)—dorsal view; (5b) Ventral view of the head of the same nymph. a = antenna; bi = basal impressions; c = crown; cl = clypeus; e = eye; f = frons; mk = median facial keels; ml = median line; sk_1, sk_2, sk_3 = side keels of prothorax, mesothorax and metathorax respectively; sn = sensoria; sp = spur; st = seta; vw = vestiges of wings; (6a) A nymph of *Criomorphus williamsi* China—dorsal view; (6b) Ventral view of the head of the same nymph; (7a) A nymph of *Criomorphus nigrolineatus* (Scott)—dorsal view; (7b) Ventral view of the head of the same nymph; (8a) A nymph of *Delphacodes pellucida* (Fab.)—dorsal view; (8b) Ventral view of the head of the same nymph.

The tergites of the abdomen are transversely striped with black; the hind margin of each tergite is white.

Delphacodes pellucida (Fab.).

The nymph (fig. 8) varies in colour from whitish-brown to dull black. The colour is usually uniform, but the thorax sometimes appears darker than the rest of the body.

Specimens collected during the winter are dull black. The vestiges of the wings appear at the second instar of the nymphs of the macropterous forms, which are commoner than brachypterous ones. This, with the uniformity of colour and the pale patch between the median keels on the crown, differentiates them from nymphs of *C. williamsi* China, which resemble them to a certain extent. Length 2·3–2·5 mm.

The crown is square. The two median facial keels are bordered with black throughout their length, but in the middle of that part of them which lies on the crown is a small pale patch. The eyes are reddish-brown. The antennae are pale brown, their second segment with black edges.

The segments of the thorax and the crown are subequal in length. The keels and the median line are pale brown bordered with dark colour. The side keels of the prothorax are bent outwards not reaching the hind margin. The legs are greyish-white or black; the first two segments of tarsi are dark, and the third is darker.

The abdomen has indistinct curved lines formed by pale patches at the mid point between the median line and the edges of each tergite.

Conomelus limbatus (Fab.).

The nymph (fig. 9) is uniformly greyish-brown, with pale patches on each side of the median line of the abdomen, half-way between it and the sides of each tergite, and forming curved lines. Length 2·1–2·35 mm.

The crown is square. The two median keels are of the same colour as the crown; the space between them is paler than the rest of the head. The basal impressions are not very distinct. The eyes are brown. The antennae are brown, their segments with black edges.

The segments of the thorax and the crown are subequal in length. The portions between the side keels are paler in colour than the rest of the thorax. The keels of the prothorax are bent outwards, not reaching the hind margin. The apodemes of the endoskeleton can sometimes be seen by transparence. The legs are pale grey in colour; both ends of each segment are darker; the tarsi are darker in colour, their first segments in fore and middle legs are black.

The abdomen from the second tergite to the seventh is of a uniform greyish-brown colour. Besides the pale curved lines on the abdomen there are pale patches on the sides of the tergites. They surround black foveae.

Delphacodes fairmairei (Perris).

The nymph (fig. 10) is white with a dark stripe on each side of its body, extending from the pronotum to the caudal end. The eyes are black and also the upper half of the frons, so that it appears as if the two black stripes passed through the eyes and were connected in front of them. Length 2·1–2·3 mm.

The crown is square. The basal impressions are not distinct. The two median facial keels are paler in colour than the rest of the frons. The upper third of the frons is black. The eyes are black. The segments of the antennae are white.

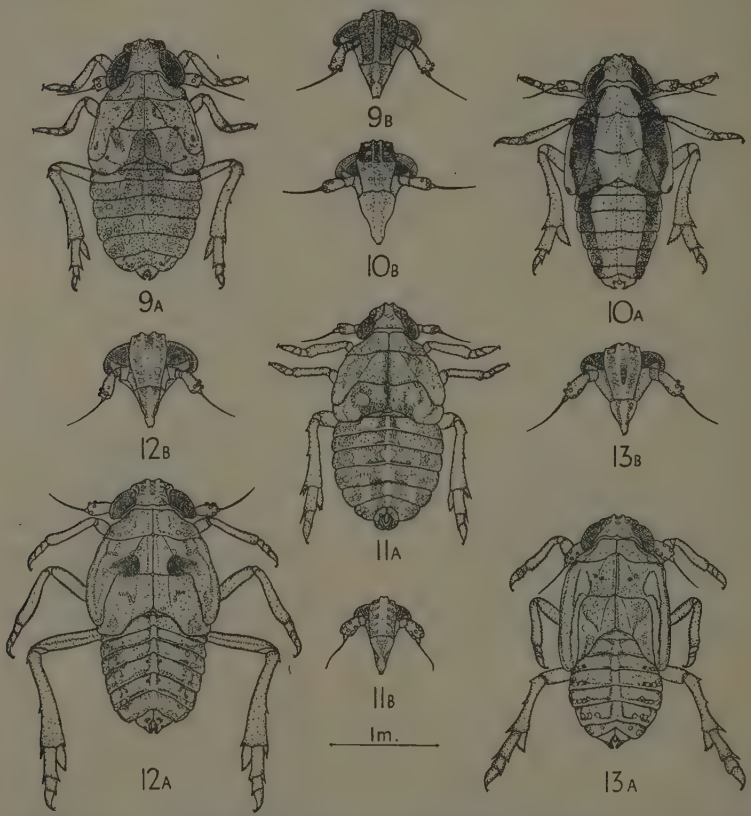
The segments of the thorax and the crown are subequal in length. The side keels of the prothorax are bent outwards, not reaching the hind margin. There are white dots in the black stripes near the lateral sides of the thorax. The legs are whitish throughout; the tarsi are darker in colour.

The abdomen is white, with a black patch on each side of each tergite. These black patches are in line with each other and with those on the thorax.

Megamelus fieberi (Scott).

The nymph (fig. 11) is white with greyish or brownish patches on the crown and abdomen and to a greater extent on the thorax. Length 2·1–2·3 mm.

The crown is about square, projecting beyond the eyes. The median keels are near to each other and have the same colour as the head. They are bordered externally with black on the upper third of the frons. The eyes are reddish-black. First segment of antennae white and the second greyish.



FIGS. 9a–13b.—(9a) A nymph of *Conomelus limbatus* (Fab.)—dorsal view; (9b) Ventral view of the head of the same nymph; (10a) A nymph of *Delphacodes fairmairei* (Perris)—dorsal view; (10b) Ventral view of the head of the same nymph; (11a) A nymph of *Megamelus fieberi* (Scott)—dorsal view; (11b) Ventral view of the head of the same nymph; (12a) A nymph of *Dicranotropis hamata* (Boh.)—dorsal view; (12b) Ventral view of the head of the same nymph; (13a) A nymph of *Delphacodes difficilis* (Edw.)—dorsal view; (13b)—Ventral view of the head of the same nymph.

The thorax is white in the middle, greyish at the sides, forming a white stripe, broader in the middle than at either end. The median line is bordered with grey. The three thoracic segments and the crown are all subequal in length, though the prothorax is rather shorter. The side keels of the pronotum are straight reaching the hind margin. The legs are dirty white near the joints; the tarsi are grey.

The abdomen is white with brown or greyish patches at the sides of tergites, sometimes

not distinct. There are two short dark-brown transverse lines on the fifth tergite near the median line.

Dicranotropis hamata (Boh.).

The nymph (fig. 12) is brownish-white with dark markings. The two median facial keels are pale, bordered with dark brown on the upper third of the frons. Length 2·3–2·5 mm.

The crown is about square. The two median facial keels are whitish, bordered with dark colour on the upper third of the frons, and with brownish-white on the lower two-thirds. The basal impressions are clear, separated by a whitish stripe. The eyes are greyish. The segments of the antennae are pale brown.

The prothorax is shorter than meso- or metathorax, which are subequal in length to each other and to the crown. The side keels of the prothorax are acute and bent outwards, not reaching the hind margin. Sometimes there are two black dots on the inner side of the side keels of mesothorax. These are the apodemes of the endoskeleton of the thorax seen by transparency. The legs are greyish-white; the segments are bordered with black; the tarsi are darker in colour.

The abdomen is whitish-brown with black markings at the sides of tergites. The median line is bordered with black.

Delphacodes difficilis (Edw.).

The nymph (fig. 13) is yellowish-white with pale grey markings; sometimes whitish-brown. The two median facial keels are darker bordered outside on the upper third of the frons; the lower two-thirds dark only between the median keels. Length 2·1–2·35 mm.

The crown is square. There is a black patch at the hind angle between the median keels on the crown. The eyes are blackish. The antennae are brownish in colour; the edges of the second segment are dark.

The meso- and metathorax and the crown are subequal in length. The prothorax is shorter. The thorax is whitish in the middle, brownish at the sides. The side keels of the prothorax are bent outwards, not reaching the hind margin. The apodemes of the endoskeleton are sometimes visible by transparency as two black dots at the inner side of the side keels of the mesothorax. The vestiges of the wings appear at the second instar. Legs are uniformly pale in colour; the edges of the segments are dark; the tarsi are darker in colour; their segments are black.

The abdomen is pale with the lateral margins of the tergites darker.

The Biology of the Adult.

The adult appears after the fifth ecdysis. The nine species here dealt with can all be identified from the work of Edwards (1896), except *Criomorphus williamsi*, described by China (1939).

The imago does not attain sexual maturity as soon as it becomes adult. Ball (1920 : 142) states, "In Hemiptera the adult emerges with eggs undeveloped and they must feed and develop them before egg laying begins." Females which die from two hours to one day after emerging from the last nymphal stage were dissected and the eggs were not yet developed. Other females were dissected after they had lived nine days or longer as adults and their abdomens were full of eggs; 18–35 in number.

When males and females were put together just after their last moult, as mentioned earlier (p. 350), they did not pair for a period which varied according to the species. In *Stenocranus minutus* (Fab.) and *Megamelus fieberi* (Scott),

which hibernate as adults, pairing occurs in March. In the rest of the species (excluding *Criomorphus nigrolineatus* (Scott) and *Delphacodes difficilis* (Edw.), whose pairing was not observed), pairing usually happens 18 to 30 days after the insect has attained the adult stage. When pairing, the male and female sit on a grass stem, in the same plane but facing different directions. I have noticed that the female always faces upwards, while the male faces downwards. The female curves her abdomen dorsally, and the male twists his and bends it latero-ventrally, so that its caudal end reaches the genital aperture of the female. Pairing lasts for 30 to 50 minutes.

Adults, as well as their nymphs, feed on grasses and rushes. *Conomelus limbatus* (Fab.) is restricted to *Juncus communis* Mey. Although I gave some of its nymphs different kinds of grasses and they reached the adult stage quite normally, the adults died quickly (after 2 to 8 days) if grass was still offered to them (p. 352). *Stenocranus minutus* (Fab.) lives on *Dactylis glomerata* L. Its nymphs died when offered other kinds of grass. The rest of the nine species feed on different kinds of grasses, such as *Holcus lanatus* L., *Agropyrum repens* Beauv., *Arrhenatherum elatus* Mert. and Koch, *Alopecurus pratensis* L., and *Lolium perenne* L.

They are gregarious insects, living in groups among their food-plant. When it happens that two or three species are located in the same spot, each species is found by itself. This gregarious habit helps the parasites to live successfully and multiply among them. The adults may be parasitised by fungi, mites and Stylopids.

Parasites.

The Delphacids are attacked by members of the orders Lepidoptera, Diptera, Hymenoptera and Strepsiptera; in addition there are fungi and mites. Perkins (1906 : xxi) gave a list of the parasites and their Delphacid hosts. In my own work I have bred a Mymarid from a Delphacid egg; a Dryinid from a Delphacid nymph; and a Stylopid from the nymphs and adults of Delphacids. Mites may be attached to and fungi grow on the bodies of the nymphs and adults. Spiders also prey on the Delphacids. Dipterous parasites were not bred in any of my collections.

Fungi.

Fungus grows on the bodies of nymphs and adults of the Delphacidae. It causes the death of the insect perhaps through blocking its spiracles. It starts its growth on excreta that have not been fully ejected, sometimes also on the body of the newly moulted nymph before it has dried. It grows also in the cavities caused by the emergences of male Stylopids It is one of the indirect ways in which the male Stylopid causes the death of its host.

Specimens with fungi were sent to Mr. T. Petch. One of them was a Stylopised nymph of *Criomorphus williamsi* China. The nymph died eleven days after the male Stylopid had emerged; a fungal mycelium grew in the cavity formed. Mr. Petch identified the fungus as *Mucor mucedo*, and notes that it is a common fungus on animal matter and is only saprophytic. Another specimen was female *Delphacodes pellucida* (Fab.) which was parasitised by two mites. It was collected from the Willow Field on 26 May 1934, and died on 1 June 1934. A fungal mycelium grew on it which Mr. Petch identified as *Cephalosporium* sp. Dr. O. W. Richards collected on 16 May 1932 a female of *Delphacodes pellucida* (Fab.) from a field adjacent to the Willow Field. It died

on 1 June and was covered with a fungus identified by Dr. M. P. Hall as *Acremonium* sp. Muir (1922) mentions a symbiosis between Delphacids and a fungus similar to *Sporosporella uvella*. He states, "All species of Hawaiian DELPHACIDAE so far examined contain them, and it appears that this organism is in no way inimical to its host. Perhaps it is beneficial, helping it to digest the starches and sugar which form a large percentage of its food."

Mites.

Only one species of mite attacking DELPHACIDAE in the Willow Field has been identified. A red mite was identified by Mrs. Hughes as a deuteronymph of *Trombidium* sp. Similar red mites, possibly the same species, are common on DELPHACIDAE and on insects of other families present in the field. The red mite is an external parasite. It attaches itself to the body of the host by means of its rostrum; takes a firm hold, and probably absorbs the host's body fluid. It leaves the body of the host when the latter is moulting, or when it is dead. The attack of the mite is not fatal. Apparently some effect is produced through shortage of nourishment for the host, so that it looks feeble.

MYMARIDAE.

Owing to lack of material, the Mymarid and Dryinid parasites will be dealt with very briefly.

Some rushes from the Willow Field were brought in on the 6 May 1935 to feed some nymphs of *Conomelus limbatus* (Fab.). The tubes containing the nymphs and the fresh rush, were put in a constant temperature room at 27° C. and relative humidity 60% on the same day. On 21 May a Mymarid was seen in one of the tubes. Three other Mymarids appeared in other tubes on the 23rd and 24th. After examining the contents of these tubes, these Mymarids were found to have emerged from the eggs of *Conomelus limbatus* (Fab.) that were present in the rushes. They were females (det. by Dr. O. W. Richards) belonging to the species *Anagrus incarnatus* (Haliday) of the type described by Bakkendorf (1925) as a variety with a long ovipositor. That author (1934) bred *Anagrus incarnatus* (Haliday) in July and beginning of August 1928 from *Conomelus limbatus* (Fab.) eggs and from eggs of *Liburnia* (*Delphacodes*) sp.

DRYINIDAE.

Dryinids commonly attack DELPHACIDAE in different localities. Richards (1933) records that he collected some nymphs of *Criomorphus pteridis* (Boh.) common on bracken at Windsor and Virginia Water and at Burnham Beeches. Some of them were found to be carrying Dryinid sacs. One female of *Dicondylus bicolor* (Haliday) was successfully reared from one of the parasitised nymphs.

On 10 April 1935 I collected from the Willow Field twelve nymphs of *Dicranotropis hamata* (Boh.). Each of them was put in a separate specimen tube, and on 11 April all the tubes were put in a constant temperature room at 27° C. The sixth and seventh abdominal tergites on the left side of one of them were deformed. This nymph moulted on the 14th. A Dryinid larva sac appeared on the 15th at the point of deformation. The nymph died on 8 May when the Dryinid larva was in the third instar. Another nymph of *Dicranotropis hamata* (Boh.) moulted on 16 April, and after the moult I saw a Dryinid larval sac between the sixth and the seventh abdominal pleura on the right side. The Dryinid larva moulted for the fourth time on 3 May 1935.

It left the body of the nymph after it had devoured all the internal organs. It crawled over the sand to the wall of the tube and started spinning a cocoon around itself. The cocoon was semi-oval and composed of woven silken threads. The larva then spun another separate layer inside the first one; it was denser and had a constriction at the middle. I could watch the changes in the larva through the glass wall of the tube. It changed to a pupa on 30 May 1935, and the adult female *Dicondylus bicolor* (Haliday) emerged on 27 June 1935.

On 13 June 1935 I collected from the Willow Field a nymph of *Dicranotropis hamata* (Boh.) having a Dryinid larval sac between the sixth and the seventh abdominal segment on the left side. I could recognise three layers on the protruding head of the sac showing that the larva had moulted three times and was in its fourth instar. The fourth moult occurred on 17 June at 11.20 a.m. The nymph was active and ran about in the tube. At 1 p.m. it stuck to one spot on the stem. After half an hour the Dryinid larva started to work its way out after it had devoured all the internal organs of the nymph. It opened the sac by exerting pressure on the head end which splits to form a slit perpendicular to the long axis of the sac. The nymph was left an empty shell. The larva protruded its head out at 1.35 p.m. with its ventral side towards the head of the nymph. By contracting and stretching itself, the larva released its body from the host, and this was completed at 1.50 p.m. The larva was whitish-yellow and glabrous. It moved to the wall of the tube and started spinning its cocoon on 18 June at 10 a.m. It changed to a pupa on 30 June, blackened and became a fully developed pupa on 6 July. A female of *Dicondylus bicolor* (Haliday) emerged on 13 July 1935. It died on 14 July 1935.

Other Delphacid nymphs, even when collected at the same time as *Dicranotropis*, have not produced any Dryinids.

Part II.

The Strepsipterous (Stylopid) parasite of the Delphacidae.

Introduction.

The parasite that belongs to the order Strepsiptera is the commonest one and attacks most, if not all, the species of Delphacidae at Slough.

Most attention has been paid to the morphological characters of the parasite, and to its biological effects on the host. I compared the males of the different Stylopid parasites that emerged from the different species of Delphacids collected from the Willow Field. I found them all identical with each other, and they appear to belong to one species. According to the tables of Pierce (1909: 70–76), it must be referred to the genus *Elenchus* Curtis, 1831. According to the descriptions and drawings made by Kirby (1815), Eaton (1892) and Perkins (1905), I refer the species to *Elenchus tenuicornis* (Kirby, 1815).

History.

Kirby (1815) described a Stylopid that had emerged from *Liburnia* (*Delphacodes*) sp. in England. He named it *Stylops tenuicornis*. S. S. Saunders (1872) placed it in the genus *Elenchus* Curtis, 1831. E. Saunders (1892) collected it in England, when the male *Elenchus* was in the act of emerging from

its puparium in the body of *Liburnia* (*Delphacodes*) sp.: Eaton (1892) also collected the male in England. Koebele (1903) (see Perkins 1905 : 90) bred specimens which he referred to *Elenchus tenuicornis* (Kirby), from *Liburnia* (*Delphacodes*) spp. in Ohio, California, and Fiji. Perkins and Koebele (1905) reared what they termed *Elenchus tenuicornis* (Kirby) in Australia. It has also been bred in different parts of the world from Delphacid hosts, but it has received different names.

Certain writers on the ELENCHIDAE have tended to give different specific names to specimens emerging from different species of the Delphacid hosts, without finding any other difference between the parasites. Thus Ogloblin (1926 : 139) found in the collection of Homoptera preserved in the Entomological Department of the National Museum of Prague, three specimens of DELPHACIDAE each bearing a single female Stylopid. He described these females as three different species of the genus *Elenchus* Curtis, but he admitted that these descriptions are of less value than they might be, as such reduced sclerotised organs as the cephalothorax of the female show few characters sufficient for the separation of the species. He studied a large series of females of *Pseudelenchus carpathicus* A. Ogl., 1925, and he was convinced that all characters of the females are liable to a great degree of variations. He named the female that was parasitic on a *Liburnia* sp. as *Elenchus dubius*; and that on *L. forcipata* (Boh.) as *Elenchus forcipatus*; and that on *L. lugubrina* (Boh.) as *Elenchus lugubrinus*.

Pierce (1909 : 167) proposed a new genus *Elenchoides*. He made his description not from a specimen, but from drawings of the cephalothorax of a male puparium and that of an adult female given by Muir (1906), who bred the type specimen from a Delphacid *Perkinsiella vitiensis* Kirkaldy in Fiji. Muir referred his specimen to *Elenchus tenuicornis* (Kirby). Pierce states that, in the absence of specimens, the species must remain defined by the host, and by the drawings published by Muir.

The same doubt also applies to another new genus founded by Pierce (1909), viz. *Pentagrammaphila* which was based on a female described as *Pentagrammaphila uhleri* found in the body of *Pentagramma vittatifrons* Uhler.

Curtis (1831 : 385) gave a description of the genus *Elenchus* which does not differ from that of *Elenchus tenuicornis* (Kirby). He named the type *Elenchus walkeri*; it was found by sweeping in England and Ireland by F. Walker and others. He stated that the minute size and the rarity of these insects had prevented him from ascertaining one or two points with the accuracy he desired.

Perkins (1910) at Hawaii bred *Elenchus melanias* Perkins from a Delphacid host; and its variety *Elenchus melanias silvestris* Perkins, also from another Delphacid host taken from very dense wet forests. It is stated that the variety approaches most nearly to *Elenchus tenuicornis* (Kirby).

Haupt (1916) in Germany bred *Elenchus* species from *Liburnia* (*Delphacodes*) sp. and he referred it to *Elenchus walkeri* Curtis.

Ahlberg (1925 : 79) bred males and females of a Stylopid from *Delphax pellucens* Fabr. (*Delphacodes pellucida* (Fab.)) and he described it as *Elenchinus delphacophilus* Ahlbg. He stated that he referred it to the genus *Elenchinus* Pierce with which it agrees perfectly except for slight differences in the formation of the thoracic sclerites. These differences, he thought, were hardly enough to form a new genus. From the only described *Elenchinus*, *E. heidemanni* Pierce, Ahlberg's species was very different. Ahlberg's description of the male, although his terminology of the parts of the metathorax is different from mine,

agrees in all structural characters, both of the thorax and of other parts, with what I consider to be *Elenchus tenuicornis* (Kirby). Even Ahlberg's figure is in agreement except that the abdomen is fatter; but this usually happens when the male is treated with caustic potash. The length of his specimen is 1·5 mm.; as in *Elenchus tenuicornis* (Kirby).

The absence of significant differences in the descriptions of males of the previous species from that of male *Elenchus tenuicornis* (Kirby), the uncertainty as to the characters of the females of the three species found by Ogloblin, its apparent occurrence in different parts of the world on Delphacid hosts, and the complete identity of all the specimens of *Elenchus* Curtis bred from different species of Delphacid hosts collected at Slough, lead me to suggest that nearly all the Stylopid parasites that have been bred out of Delphacids, belong to one species *Elenchus tenuicornis* (Kirby). Perkins (1905 : 90) stated with regard to the species that he called *Elenchus tenuicornis* (Kirby), " While in Australia we found the same to be very common in every locality which we investigated, and to attack not only *Liburnia* (*Delphacodes*) but several other genera of Delphacid leaf hoppers."

The following example is probably an exception to the previous generalisation. Koebele bred a Stylopid species from *Liburnia* (*Delphacodes*) *campestris* (Van Duzee), and from *Liburnia* (*Delphacodes*) *lutulenta* (Van Duzee) in 1903 at Columbus, Ohio. In his notes (see Perkins, 1905) he referred it to the genus *Colacina* Westw. (but the host of this parasite (Westwood, 1877) was not a Delphacid). Perkins (1905) corrected its name and referred it to *Elenchus tenuicornis* (Kirby). Pierce (1909) included it as a type of a new genus *Mecynocera* Pierce, and described the species as *M. koebelei* Pierce. Pierce (1918 : 481) changed the name to *Liburnelenchus koebelei* Pierce. The principal differences that he found are in the dorsal side of the 9th abdominal segment; in the maxillary palps which are feebly two-segmented, the first segment bearing about its middle a filiform process with a knobbed apex, reaching the tip of the second segment. Neither Koebele nor Perkins described such structures in the specimens. It may be noted that in my specimens of *Elenchus tenuicornis* (Kirby) the second segment of the maxillary palpi is much longer than the first; in Pierce's figure the proportions of the segments are reversed.

Life-cycle.

Elenchus tenuicornis (Kirby), like the other members of the order Strepsiptera, is viviparous. Out of the fertilised eggs, found in the body of the female, hatch triungulinids which pass out through the genital pores to the brood pouch. They then pass outside through a special opening in the cephalothorax of the female. The triungulinids infect Delphacids in whose bodies they undergo a hypermetamorphic development.

The triungulinid changes its form, which is oligopod or campodeoid, into a scarabaeidoid and then to grub-like or apodous type. They grow and moult; and before they reach the pupal stage, they pass through a prepupal stage. The prepupa of the male can easily be recognised as it shows wing-pads, rudiments of legs, and its abdomen is slender and tapers towards the caudal end. Probably this stage is not present in the life-cycle of the female which never pupates, but metamorphoses gradually into the grub-like adult, whose existence terminates with the liberation of the triungulinid larvae.

The life-cycle best described hitherto [1] is that of *Xenos vesparum* (Rossi)

[1] When the above account was written. Since then, Kirkpatrick (1937) has published an account of *Corioxenos antestiae* Blair parasitic on *Antestia* (PENTATOMIDAE).

observed by Nassonow (1892). He states that the larvae of the male and female of this species follow different lines of development after the second instar. They have seven instars. He described the seventh instar of the male larva as a pupa, because the appendages have become strongly developed. Again he mentions that this pupa moults and the second or real pupa was formed within its skin. In my account the first " pupa " is termed the " prepupa."

For the purpose of obtaining the different stages of the larva, nymphal and adult Delphacids were collected on 26 August 1935 from a spot in the Willow Field from which I had never collected any stylopised Delphacid before the experiment (nor was any stylopised specimen collected afterwards from there). Three hundred and fifty Delphacids were collected; 321 of them belonging to the species *Conomelus limbatus* (Fab.), the most abundant species of DELPHACIDAE in the field at that time of the year. All the insects were put in a tube containing a female *Criomorphus williamsi* China, infected by a female *Elenchus*, the triungulinids emerged at 4 p.m. on the same day. Fifty-four adults and nymphs were found dead the next day, and were pickled in alcoholic glycerine. Each succeeding day some of the adults were pickled. Later the nymphs that had changed to adults were preserved also.

A shrunken type of triungulinid larva was found in 39 adults and 24 nymphs pickled one to seven days after infection. I describe this form under the scarabaeidoid larva (p. 367). The real scarabaeidoid type of larva was found in 21 adults and 9 nymphs amongst the specimens preserved 8 to 9 days after infection. An apodous type of larva was found in 5 adults and 2 nymphs amongst the specimens pickled 10, 11, 13, and 23 days after infection. On dissecting the other 62 Delphacids that had been preserved between the 10th and 23rd day, 11 were found to contain scarabaeidoid larvae. It is impossible to be certain whether these previous stages belong to the male or to the female. The characters given by Nassonow for such separation, *e.g.*, the different degree in the fusion of head and thorax, are not visible here. In the advanced apodous larvae, the formation of the hemispherical cephalothorax of the puparium indicates that such a larva is a male. In a nymph of *Conomelus limbatus* (Fab.) preserved 23 days after infection, I found an advanced male apodous larva with the cephalothorax of its puparium well developed, though internal. Another advanced stage of apodous larva was found in the same host and differed completely from the previous one. It has been treated as an advanced apodous larva of the female, as there was no hemispherical cephalothorax characteristic of the male puparium, nor any distinct larval head as shown in the male.

A male prepupa was found in a nymph of *Conomelus limbatus* (Fab.) preserved 31 days after infection. This corresponds to the seventh instar in the description of Nassonow. He stated that in *Xenos* during this stage the cephalothorax of the male puparium is pushed outside the body of the host and the pupal stage is reached inside the skin of this instar. After maturation the adult male emerges, and the cephalothorax of the female appears outside the body of the host. In *Elenchus* the cephalothorax of the male puparium is pushed outside when the pupal stage has just been attained. The pupa is white in colour when dissected out. The following are descriptions of the different stages in the life-cycle.

The egg.

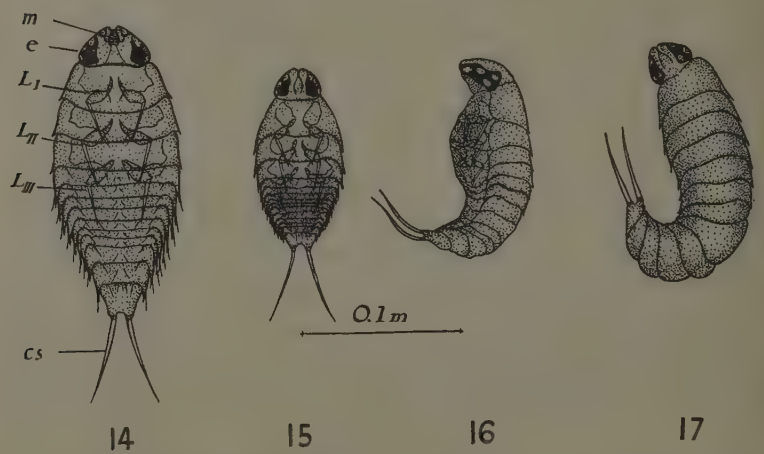
The egg of *Elenchus tenuicornis* (Kirby) is oval in shape. Its long diameter is 0·068 mm.

The female contains 1450–1500 eggs. I counted the eggs in female parasites dissected out of two females of *Conomelus limbatus* (Fab.); each contained about 1450 eggs.

Three others from a female *Conomelus limbatus* (Fab.), and from two reduced males of *Criomorphus williamsi* China, each contained about 1480 eggs; two others dissected from one reduced male of *C. williamsi* China, and from one reduced male of *Dicranotropis hamata* (Boh.), each contained also about 1480 eggs; and in one dissected from a reduced male of *Delphacodes pellucida* (Fab.), there were 1493 eggs. The average number of eggs is therefore about 1475.

The Triungulinid.

The name given by Chobaut to the first stage of a stylopid larva is "Triungulinid" because it resembles the Meloid triungulin. The triungulinids hatch from the eggs inside the body of the female, find their way to the exterior through the opening of the brood pouch, and crawl over the mother host, *i.e.*, the host that has a female parasite in its body. This is the free living phase in the life of the Stylopid larva.



FIGS. 14–17.—(14) A triungulinid larva. cs = caudal seta; e = eye cluster; L_I, L_{II}, L_{III} = fore, middle, and hind legs; m = mouth; (15) A shrunken triungulinid larva; (16) A scarabaeidoid larva—lateral view; (17) A scarabaeidoid larva—dorsal view.

The triungulinid (fig. 14) is campodeoid in form; yellow in colour; oval in shape; slightly convex, tapering towards each end. Its length is 0·180–0·183 mm., and with the caudal setae it measures 0·239–0·241 mm. The eye clusters on each side of the head are remarkable. They are black with the facets transparent and hexagonal. The mouth opens at the anterior end. The three thoracic segments are large; each bears a pair of well-developed legs; all the legs are alike in structure; the coxae are large; the femora short and stout, and each bears a spine at its anterior end. The leg ends in two spines; one is straight and long and the other is short and is attached at the distal end of the first spine. The abdomen is grooved on the ventral side. There are ten abdominal segments smaller than those of the thorax. Every segment bears a seta on each side, and one on each side of and near to the ventral median line. The ninth sternite bears a row of setae at its posterior margin. The edge of each tergite is produced backwards into short lateral spines. The body terminates at the caudal end with a pair of long setae.

The scarabaeidoid type of Larva.

The shrunken triungulinid form (*fig.* 15).

When the triungulinid gets into the body of the host, its body shrinks and the abdominal segments get smaller and narrower. The larva still retains all its organs. All the setae on the lateral and ventral sides of the segments, and also the caudal setae, are present. The legs with all their segments are preserved. The eye clusters are prominent. There are still three thoracic segments and ten short abdominal ones. Length 0·112–0·115 mm.

The real scarabaeidoid form (*fig.* 17).

The larva then starts to change to a scarabaeidoid form. The abdomen becomes more flexed ventrally at the anterior end. The setae are lost; the legs are still present, and also the eye clusters. There are still three thoracic and ten abdominal segments, all equal in size, except the first thoracic segment, which is still larger; the head is not fused with it. Length 0·127–0·151 mm.

The apodous type of larva.

The larva moults late and changes to an apodous type (fig. 18). The body becomes cylindrical, still with thirteen segments, all of the same size. It becomes whitish in colour. The head is not large and has two red spots representing the eye clusters of the early larva. There is no trace of legs or of setae. Length 0·34 mm. In the next stage (fig. 19), the larva is free from its exuviae and the body is white and cylindrical. The head still does not show any structure beside the red eye spots. Length 0·47–0·48 mm.

After this stage the larva, when it moults, does not shed the exuviae, but retains them to form a puparium.

In an older stage, the head becomes sclerotised; segmentation is very feeble; the body is straight and tends to taper towards each end.

The next stage discovered was one belonging to the male (fig. 20). The larva is loose in the puparium. Its head fills the cap of the puparium, which is sclerotised, and is easily detachable. The wall of the puparium shows two layers. Probably the inner layer represents the exuviae of the previous stage not fused with the wall of the puparium. The puparium still shows segmentation, while the larva shows it very feebly. Length of larva 0·845 mm. and length of puparium 1·090 mm.

The advanced apodous larva of the female (fig. 21) had no puparial cap. The top of its head showed through the puparial wall. The rest of the head was inside the puparium, like the rest of the body, and was more sclerotised. There were two red spots representing the eyes of the larva, and also two pairs of analogues of the legs, which showed that the first two thoracic segments had fused with the head. The third thoracic segment was still clear and separate from the cephalothorax. There were ten abdominal segments. The first was large; the next three were sclerotised. They are the only distinct segments present in the adult female. The rest of the abdominal segments tapered towards the caudal end and lay loose in the puparium. The puparium was large; its inner end was in contact with the filter chamber of the host. There was a groove extending along the abdomen of the larva. This perhaps would later form the brood pouch of the adult female.

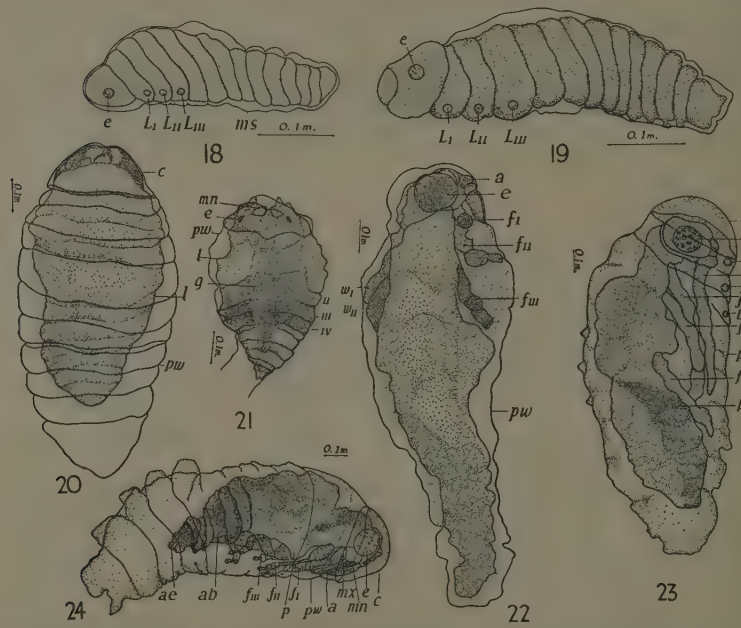
The Prepupa of the male.

The prepupa (fig. 22) is also loose in the puparium, which shows the exuviae of the previous stage unfused with its wall; the cap is of one layer and strongly sclerotised. This suggests one of two alternatives; either the exuviae of the previous stage but one is shed, or they are fused with the following exuviae. The second alternative is the most probable one, as the outer puparial skin looks harder than that of the previous advanced eruciform

male larva. It is usually ruptured at its end near to the filter chamber of the host. Eye rudiments, wing-pads, and leg rudiments are all present. Segmentation is beginning. The abdomen is more slender than the rest of the body. Length 1·384 mm.

The Pupa of the male.

In the pupa the external organs of the adult are well represented. When the larva changes to a pupa, the body is white and not yet sclerotised (fig. 23). The eye clusters are



Figs. 18–24.—(18–19) Apodous larvae. e = eye spot; L_1, L_{11}, L_{111} = rudiments of fore, middle, and hind legs, respectively; ms = moulted skin; (20) An advanced male—apodous larva. c = cephalothorax; l = larva; p.w. = puparial wall; (21) An advanced female—apodous larva. e = eye spot; g = groove; l = large; mn = vestiges of mandibles; p.w. = puparial wall; II, III, IV = second, third and fourth abdominal segments respectively; (22) A male prepupa. a = vestiges of antennae; e = eye; f_1, f_{11}, f_{111} = vestiges of fore, middle and hind legs; p.w. = puparial wall; w_1, w_{11} = vestiges of wings; (23) A young male pupa. a = antenna; c = cap of puparium; e = eye; f_1, f_{11}, f_{111} = fore, middle and hind legs; L_1, L_{11}, L_{111} = rudiments of legs of larva; p = pupa; p.w. = puparial wall; (24) An advanced male pupa. ae = aedeagus; mn = mandibles; mx = maxillary palps. The rest of lettering as in fig. 23.

big with the facets quite clear. The antennae and legs are present but not completely developed. Segmentation of the abdomen is not clear. The puparium is sclerotised at its anterior end at the cap; its inner end is in contact with the filter chamber. Length of pupa 1·375 mm. Long diameter of cap 0·5 mm.; and the cap protrudes outside the body by about 0·125 mm.

After this the pupa becomes heavily sclerotised and becomes darker in colour (fig. 24) and the appendages are completely developed.

The Male.

The body (fig. 25, A) is slender and black, with long brown legs, brown flabellate antennae and hyaline-smoky wings. Length 1·5 mm.; expanse of wings 3·3 mm. Head subquadrangular, transverse; its breadth 0·4 mm. Vertex depressed near the eyes. Eyes large, occupying the whole lateral side of the head, subsessile, composed of isolated facets, 20 in number, and separated by spaces covered with stiff black hairs. The antennae arise from the anterior end of the head, far from the eyes. They are brown in colour, covered

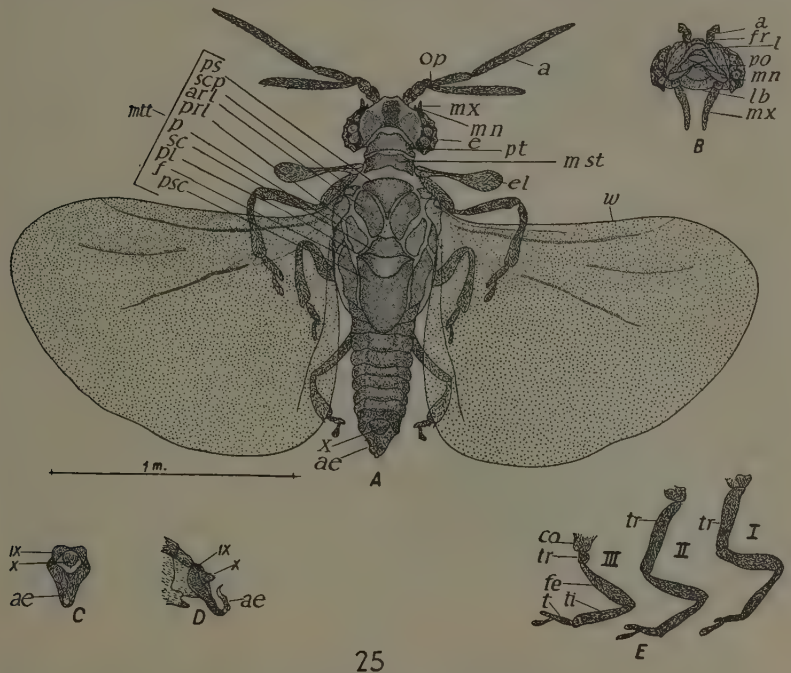


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FIG. 25.—Male *Elenchus tenuicornis* (Kirby).

A = Dorsal view of the male. B = Ventral view of head. C = End view of the caudal end. D = Lateral view of the caudal end. E = Legs.

a = antennae; ae = aedeagus; Arl = anterior lumbium; co = coxa; e = eye; el = elytra; f = femoralium; fe = femora; fr = frons; l = labrum; lb = labium; mn = mandibles; mst = mesothorax; mtt = metathorax; mx = maxillary palps; op = olfactory pit; p = pleura; pl = postlumbium; ps = praescutum; psc = postscutellum; pt = prothorax; sc = scutellum; scp = scapula; t = tarsus; ti = tibia; tr = trochanter; w = wing. I, II and III = fore, middle and hind legs; IX and X = ninth and tenth abdominal segments.

with sensory hairs, and composed of five segments. The first two segments are very short; the first is cup-shaped and the second globose. The third segment is very short and produced laterally into a long flabellum reaching nearly to the middle of the fifth segment. There is an olfactory pit at the base of the flabellum. The segment is cupped at the distal end to receive the fourth segment. The fourth and fifth segments are long; the fifth is twice as long as the fourth. Length of antennae 0·8 mm. The frons (fig. 25, B) is very narrow and occupies the portion between the antennae. It is shortened by the

enlargement of the oral aperture which occupies nearly all the front and ventral sides of the head. The oral aperture is triangular, with one side of the triangle ventral. The mouth-parts are very much reduced. The labrum is represented by a small flap at the lower edge of the frons. The mandibles are long, stout, curved slightly outwards near the tip which is pointed. They measure 0·1 mm. in length. The maxillae are represented by the two-segmented palpi. The first segment is very short and the second is long, covered with sensory hairs. They are larger than the mandibles, 0·2 mm. in length. The labium is not distinctly developed. The opening of the pharynx can be seen in the centre of the oral aperture. It is small and oval in shape. The pro- and mesothorax are narrow rings; the second carries, in addition to the legs, the elytra on each side. The elytra are ladle-shaped, with only one vein. The metathorax is large, as long as the abdomen. Length 0·6 mm. It has a shape peculiar to the genus. The terminology of its parts is that used by Pierce (1909 : 65). The prescutum is triangular with one side curved and directed anteriorly. The scutellum is subquadrangular and separated from the prescutum by a membraneous area. It is followed by another membranous portion, the postlumbium. The scutum is composed of four sclerites (the lumbia); two on each side of the prescutum and scutellum. Each anterior lumbium is quadrangular and adjacent to the prescutum; and each posterior lumbium is triangular with one side near the scutellum. There is a small quadrangular sclerite at the base of the wing called the "scapula." The post-scutellum is triangular in shape, with one side emarginate and directed anteriorly; its posterior margin is obtusely rounded and produced behind, reaching to the hind margin of the second abdominal segment. Behind the lumbia and postscutellum are the pleura and femoralia. The wings are always expanded. When at rest, they are held perpendicularly over the body. Each is a quadrant of a circle, hyaline-smoky in colour, with black veins, four extending from the base and a fifth one near the distal end between the second and the third veins. The fore and middle legs (fig. 25, E) have long slender trochanters resembling the femora. The trochanters of the hind legs are very small and globose. The coxa of each leg is broad; the tarsi have two segments; the second is attached near the distal end of the first. The legs are covered with soft hairs. The abdomen has ten segments, the ninth one, seen in caudal view, is wide, pentagonal. The tenth segment (fig. 25, C and D) is short and rounded, resembling a pair of fused cerci. The aedeagus is attached to the sternal side of the ninth segment. It is stout and heavily sclerotised except at its tip, which is slightly hooked.

The Female.

The body (fig. 26, A) is grub-like, and fills the abdominal cavity of the host, being prolonged into a slender portion in the host's thoracic region between the muscles. There are two slightly sclerotised peg-like processes on the ventral side at the posterior ventral margin of the metathorax of the host. These fix the female firmly in the body of the host. The other sclerotised parts of the body are the cephalothorax and the first four abdominal segments. The rest of the body is white and not sclerotised. The cephalothorax is the only part of the female protruding from the host (fig. 26, C). In front view, the cephalothorax (fig. 26, B) is disc-like with two semicircles facing each other. One is light in colour, and small, and directed towards the anterior end of the host. This is the opening of the brood pouch; there is a ring-shaped spiracle at each corner of it. Its posterior margin is formed by the pro- and mesothorax followed by the metathorax which is produced anteriorly and surrounds the spiracle.

The other semicircle is larger and dark; and directed towards the posterior end of the host. Its anterior part (*i.e.*, anterior on the female itself) is dark brown with two light brownish spots at the sides where the pores of Nassonow's glands exist. They are in two groups of about 12 pores each. At the lateral side of each spot, traces of antennae can easily be seen. The posterior part is light brown with the mouth-parts in the middle.

The mandibles are transverse, horseshoe shaped with longer anterior branch. They enclose the mouth opening. The labrum lies between them at their anterior edges. It is thin; and the space anterior to it is full of pores. There is a sclerotised part in the middle of the posterior edge of the semicircle, facing the mandibles. This corresponds to the labium. In a lateral view, the cephalothorax appears lobed and ridged. There are three apertures in the second, third and fourth abdominal segments respectively. These are the

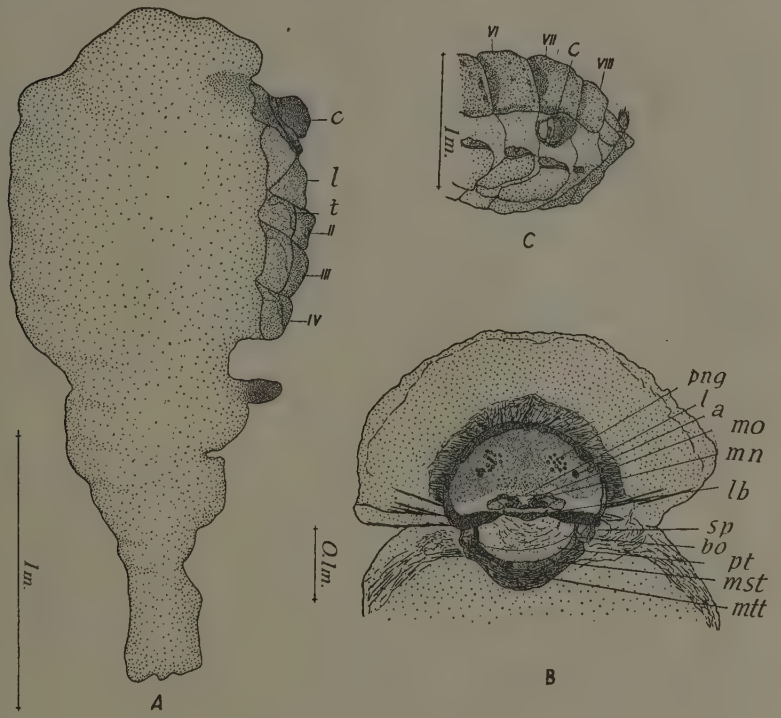

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FIG. 26.—Female *Elenchus tenuicornis* (Kirby).

A = Lateral view of the whole body of the female. B = Front view of the cephalothorax. C = Lateral view of a part of the abdomen of a Delphacid, showing the cephalothorax of the female parasite.

a = rudiments of antennae; bo = opening of the brood pouch; c = cephalothorax; l = labrum; lb = labium; mn = mandibles; mo = mouth opening; mst = mesothorax; mtt = methathorax; png = pores of Nassonow glands; pt = prothorax; sp = spiracle; t = trumpets. I to VI = first to sixth abdominal segments.

genital apertures through which the newly hatched young pass from the body cavity to the brood pouch.

Measurements of the different parts of the female: length of cephalothorax, 0·24 mm.; breadth of cephalothorax, 0·234 mm.; length of mandibles, 0·048 mm.; breadth of mandibles, 0·012 mm.; breadth of mouth opening, 0·018 mm.; length of spiracles, 0·030 mm.; breadth of spiracles, 0·027 mm.; distance between spiracles, 0·132 mm. (*i.e.*, breadth of the opening of the brood pouch); length of the opening of the brood pouch, 0·060 mm.

The Life History.

The following remarks summarise collections and observations carried out during nearly every week throughout the summer.

The eggs are found filling the body cavity of young females. They stay there till they are fertilised, and hatch out as triungulinids which emerge from the body of the female through the genital pores. They pass first into the brood pouch between the body of the female and its pupal skin, and then through a slit posterior to the mouth opening. The female is situated with her ventral side upwards so that when the young come out, they crawl over the body of the mother host. Usually the mother host is found where there are many nymphs. So when the triungulinids come out, they easily find nymphs into which they can burrow quickly. They may also penetrate adults if there are not enough nymphs to infect. Triungulinids are short-lived. In three females out of 47, the triungulinids emerged in the laboratory in each case at about 4 p.m. The next morning all the triungulinids left were always found dead. All the tubes containing the stylopised specimens were examined daily but only in three tubes were the triungulinids found. One of them contained a female *Criomorphus williamsi* China which was collected on 9 July 1934; the triungulinids emerged on the 11th at 4 p.m., and the host died on 12 July 1934. Another tube contained a reduced male *C. williamsi* China, which was collected on 16 July 1934; the triungulinids emerged on the 17th at 4.10 p.m., and the host died on the 18th. The third tube contained a reduced male *C. williamsi* China, which was collected on 23 July 1935; the triungulinids emerged on the 26th at 3.50 p.m.; and the host died on 27 July 1935.

The rarity with which triungulinids were seen to emerge did not allow me to repeat the experiment to obtain a complete series of the stages of larvae.

The cap of the male puparium, when it appears, is dark brown in colour, and the head of the pupa can easily be seen through it. After two hours, it becomes opaque and black. The male pupa develops with its ventral side upwards, so that when the male emerges, it is easy for him to hang on the body of the host until his wings are dry. The time between the first appearance of the cap of the puparium outside the body of the host and the emergence of the male differs according to the time of the year. At the beginning of the summer, in May, it is longer; on the average 23 days. In middle and in late summer, from June to August, the average period is 12 days only (8–18 days).

Table IV shows: (1) the date of appearance of the male puparium in different nymphs, and (2) the date of emergence of the male; also (3) the length of the life of the host after the emergence of the male parasite, the latter is referred to later in connection with the effect of the parasite on the host (p. 379).

The average period elapsing between the time at which the Delphacid nymph changes to adult and the appearance of the cephalothorax of the female parasite is about 14 days as can be seen in Table V, which gives (1) the date of the last moult, (2) the date of the appearance of the cephalothorax in the different species of Delphacidae, and (3) the time in days between (1) and (2).

Behaviour of the male.

When the male is ready to emerge, it pushes off the cap of the puparium. The cap sometimes falls off, but in other cases it remains attached by a hinge at the posterior side of the puparium. By means of peristaltic movements, the male emerges. It hangs for a short time to the host while its wings spread and get dry, and then starts its short active life, flying here and there searching

TABLE IV.

Host-species	Date of collection	Date of death	(1)	(2)	Time in days between (1) and (2)	(3) in days
C. williamsi China .	31.v.34	29.vi.34	1.vi.34	10.vi.34	9	19
,, ,, .	23.iv.35	8.vi.35	10.v.35	2.vi.35	23	6
,, ,, .	26.iv.35	30.v.35	2.v.35	26.v.35	24	4
,, ,, .	22.v.35	29.vi.35	9.vi.35	23.vi.35	14	16
,, ,, .	27.v.35	29.vi.35	12.vi.35	23.vi.35	11	16
,, ,, .	30.v.35	20.vi.35	3.vi.35	18.vi.35	15	2
,, ,, .	3.vi.35	21.vi.35	4.vi.35	20.vi.35	16	1
,, ,, .	4.vi.35	30.vi.35	16.vi.35	24.vi.35	8	6
C. nigrolineatus (Scott)	2.v.35	2.vi.35	9.v.35	31.v.35	22	2
D. hamata (Boh.) .	31.v.34	24.vi.34	3.vi.34	15.vi.34	12	9
,, ,, .	10.iv.35	18.vi.35	22.v.35	9.vi.35	18	9
,, ,, .	23.iv.35	18.vi.35	28.v.35	11.vi.35	14	9
C. limbatus (Fab.) .	3.viii.34	24.viii.34	9.viii.34	19.viii.34	10	5
,, ,, .	26.vii.35	28.viii.35	12.viii.35	25.viii.35	13	3
,, ,, .	26.vii.35	16.viii.35	4.viii.35	12.viii.35	8	4
,, ,, .	5.viii.35	20.viii.35	5.viii.35	14.viii.35	9	6

TABLE V.

Host-species	Date of collection	(1)	(2)	(3)
C. williamsi China . . .	14.v.34	22.v.34	9.vi.34	17
,, ,, . . .	14.v.34	27.v.34	9.vi.34	12
,, ,, . . .	21.v.34	26.v.34	12.vi.34	16
,, ,, . . .	30.v.34	8.vi.34	21.vi.34	13
D. fairmairei (Perris) . .	9.vii.34	13.vii.34	26.vii.34	13
D. hamata (Boh.) . . .	3.vii.34	9.viii.34	23.viii.34	14
C. limbatus (Fab.) . . .	22.viii.34	26.viii.34	6.ix.34	11
,, ,, . . .	26.vii.34	27.vii.35	6.viii.34	11

for a female. I watched a male emerging from a nymph of *C. williamsi* China. The nymph was collected from the field on 2 May 1935; the cap of the male puparium appeared on 9 May and the male *E. tenuicornis* (Kirby) emerged at 10.50 a.m. on 31 May. The nymph was disturbed and ran about in the tube. This caused the male to fall down on the sand at the bottom of the tube before it was completely dry. It stuck to the sand, and began moving its abdomen dorso-ventrally. I transferred it to a clean tube. The abdomen did not move, nor did the antennae which diverged to form a V. At 12.10 p.m. it settled on the sides of the tube. The wings were vibrating continuously with short intervals of rest; sometimes the elytra vibrated in the same rhythm as the wings. The end of the abdomen sometimes moved upwards and downwards and its caudal end was pressed on the side of the tube. Sometimes it stopped walking and the front legs moved as if in the act of digging. The maxillary palpi and mandibles were always extended outwards. At 12.45 p.m. the antennae, maxillary palpi, and mandibles started moving in all directions. The middle and hind legs showed weakness and could not take as firm a hold as before;

the abdomen was still bent forward, and its caudal end stuck to the side of the tube. The front legs were still moving in the same characteristic way. The elytra were bent downwards, and the wings upwards, motionless. It could not stand on its feet for long at a time. At 1 p.m. it became active again and walked about, and then became weak and lay on its side. It repeated this several times till 3 p.m. During that time the abdomen was continuously bent ventro-anteriorly, moving from left to right. Its front legs and antennae occasionally moved feebly. At 3.30 p.m. there was no sign of movement and the male was dead.

I watched other males emerging from different hosts and they all behaved exactly the same. Thirty-nine males emerged during the course of my work; 22 emerged before 9 a.m.; 8 at about 9.30 a.m.; 6 at about 11 a.m.; 2 at about 1 p.m.; and one at 3.30 p.m. Thus the male usually emerges early in the morning before 9 a.m. The males lived for a short time only, from four to five hours. They took no food.

Remarks on copulation.

The female is rooted in the body of the host, with only the cephalothorax appearing outside, apparently waiting to be fertilised. I was not fortunate enough to observe the process of fertilisation in the laboratory or in the field. The twenty-two males that emerged in the laboratory from June to September 1935 were put in tubes containing Delphacids infected with female parasites. The hosts of these females had either been collected at different times with the female parasite already visible on their bodies or the female parasites had appeared at different dates in the laboratory. But the males never paid any attention to the females, and fertilisation never occurred. The tubes were watched most of the time the male was alive. Perkins (1918 : 129) states, "Many female Stylops entirely failed to attract any male, and it is evident that only certain individuals have, or at any rate, exert this power, this probably depending on their age or the state of development of the ovaries."

This might suggest that parthenogenetic development occurs here, but an observation shows that this is very unlikely. A nymph of *C. williamsi* China was collected on 14 May 1934; on 25 May it moulted to an adult female, and the female parasite appeared on 3 June, a male parasite was put in the tube on 5 June; no fertilisation was noticed. The host died on 28 July 1934. When dissected, the female *Elenchus* was found to contain eggs, although its host died 54 days after the appearance of the female parasite; a time long enough for the triungulinids to hatch out if they develop parthenogenetically. This may be compared with the data in Table VI (p. 375), *e.g.*, a female of *C. williamsi* China collected on 14 May 1934 died on 29 June 1934; when dissected, it was found to contain triungulinids. Four other females were dissected out after they had lived from 35 to 49 days and they still contained eggs. So it appears that fertilisation is essential for the development of the egg. Muir, in speaking of the activity of males of *Elenchoides perkinsi* Pierce (*Elenchus tenuicornis* Muir *nec* Kirby, in my account (p. 363) I suggest that it was an example of *Elenchus tenuicornis* (Kirby)), described the process of copulation. He describes how it disturbed the host which flicked its abdomen to shake off the male parasite which was able to spring upon the host's abdomen and attach itself to the female parasite. Muir stated that he had never seen the male *Elenchus* retain its hold of the female for more than six seconds; generally it was attached only two or three seconds. He was unable to say if fecundation took place during that time or exactly how copulation occurs. As dissection

proved that eggs must be fertilised to develop, fecundation must have happened during the time while the male is attached to the female, though very short.

Schrader (1924) proved that *Acroschismus wheeleri* Pierce reproduces sexually, although Brues (1903), working on the same species, claimed that it reproduced parthenogenetically. Smith and Hamm (1914) working on *Stylops melittae* Kirby also concluded that parthenogenesis was probable. Schrader followed three lines of investigation: (1) continuous collecting throughout a period of three years; (2) breeding experiments under close observation in the laboratory and (3) the cytological examination of all material produced by means of the first two methods. She proved by each line of investigation that fertilisation must occur. The first two lines were followed up in *Elenchus tenuicornis* (Kirby), and although copulation was never observed, yet dissections of the females make it very likely that fertilisation occurs.

Number of generations per year.

E. tenuicornis (Kirby) passes the winter in the larval stage. Adults and nymphs of Delphacidae collected during the winter months were found to contain triungulinids in the scarabaeidoid form. Twenty-three such larvae were found in 192 nymphs collected in November, and dissected as they died in the spring. The adults first appear in the beginning of June. Two of the nymphs mentioned above were kept in captivity during the winter. The cap of male puparia appeared on their bodies during May and the adult males emerged in the beginning of June. Another two nymphs, that were kept in captivity during the winter, changed to adults on 22 and 27 May 1934, and the cephalothorax of the female parasite appeared on their bodies on 9 June 1934. Further, seven out of a number of nymphs collected on 7 April 1935 showed male puparia in May and adult *Elenchus* emerged in June.

The female parasites that were found late in June and early in July were full of triungulinids. Table VI gives a list of some of the infected adult Delphacids that were collected but died before the emergence of the triungulinids; on dissection, they were found to contain female parasites full of triungulinids.

Table VI.

Host-species	Sex	Date of collection	Date of death
C. williamsi China	♀	14.v.34	29.vi.34
,, ,, ...	reduced ♂	23.v.34	6.vii.34
D. pellucida (Fab.)	reduced ♂	29.v.34	8.vii.34
C. williamsi China	♀	19.vi.34	27.vi.34
D. fairmairei (Perris)	♀	9.vii.34	15.vii.34
C. williamsi China	reduced ♂	9.vii.34	16.vii.34
,, ,, ...	♀	16.vii.34	22.vii.34
,, ,, ...	reduced ♂	24.vi.35	14.vii.35
,, ,, ...	reduced ♂	5.vii.35	23.vii.35
,, ,, ...	♀	5.vii.35	14.vii.35
,, ,, ...	♀	17.vii.35	22.vii.35

From Table VI it can be seen that the triungulinids emerge about the end of July. The three cases of the emergence of triungulinids occurred in the laboratory at the first half of July (see p. 372). At that time, the field is full of nymphs, mainly of *Conomelus limbatus* (Fab.), so the triungulinids find suitable

hosts to infect. Sometimes the mother host has been found among the nymphs of *C. limbatus*.

Female parasites with mature triungulinids are also found late in September and in October as Table VII shows. It gives a list of the dates of collection and death of adult parasitised *C. limbatus*.

Table VII.

Host-species	Sex	Date of collection	Date of death
C. limbatus (Fab.)	♀	14.viii.34	16.viii.34
,, ,,	♀	22.viii.34	20.ix.34
,, ,,	♀	4.ix.34	19.ix.34
,, ,,	♀	4.ix.34	16.ix.34
,, ,,	♀	3.ix.34	14.ix.34
,, ,,	♀	7.ix.34	20.ix.34
,, ,,	♀	7.ix.34	25.ix.34
,, ,,	♀	7.ix.34	9.x.34
,, ,,	♀	13.ix.34	29.ix.34
,, ,,	♀	25.ix.34	12.x.34

At that time of the year, the field is full of nymphs mainly of *C. williamsi* China, *D. pellucida* (Fab.) and *D. hamata* (Boh.). These are infected and the triungulinids pass the winter in them.

All these data are summarised in Table I, showing the relation between the different stages of the Delphacids and this parasite all the year round.

This shows that *E. tenuicornis* (Kirby) has two generations a year; one with a short period of three months only; and the other with a long period of nine months. In June, females full of eggs may be found. The eggs mature and the triungulinids hatch and leave the mother host. New hosts are infected and in these they become adult. The females of the second generation contain eggs in September; their triungulinids leave the mother host, infect other hosts, and complete the rest of the life-cycle during autumn, winter and spring.

Table VIII shows the number of parasites and the percentages of adult males and females in each month from May to October during the time observations were made.

Table VIII.

	May	June	July	Aug.	Sept.	Oct.
No. of parasites	12	45	16	4	15	15
No. of males emerged	4	34	4	1	10	4
% of males	33·3	75·6	25	25	66·7	26·7
No. of females	8	11	12	3	5	11
% of females	66·7	24·4	75	75	33·3	73·3

Collection of Specimens.

E. tenuicornis (Kirby), like most members of the order Strepsiptera, has two free stages. One is the free living triungulinid. This is minute, measuring 0·2–0·25 mm. in length, yellow in colour, and more or less transparent, so it is very difficult to find in the field. Moreover, the triungulinids emerge late in the day, at about 4 p.m. The second free stage is the male

which emerges early in the morning, lives from four to five hours and then dies. In this short time, it is busy searching for the female. This, in addition to its small size (1·5 mm.), would make it very hard to see the male in the field; even if captured in a net it would be easy for it to find its way out through the meshes. Pierce (1909) mentions a few records of collecting the male on the wing. I have never seen males in the open myself.

The easiest way to obtain specimens of *E. tenuicornis* (Kirby) is to breed it from its hosts. The infected Delphacids show the cephalothorax of the male or of the adult female quite clearly.

In determining percentage parasitism by *Elenchus*, the following specimens have been considered: (*a*) collected specimens which were examined for the parasite puparium or cephalothorax, and (*b*) specimens dissected in the search for larval stages. These amount in all to 1008 Delphacid specimens.

In Table IX is shown the number of Delphacids of each species collected from the Willow Field (except *Delphacodes difficilis* (Edw.), which is very rare there), the number and sex of adults, the number of nymphs; the number of stylopised specimens in each case and the percentage of stylopisation.

It was noticed during the collection that stylopisation occurs at certain parts in the Willow Field and not in others. Usually these spots are those where the food-plants of the different species of Delphacids occur together.

TABLE IX.

	Delphacids	*C. williamsi* China	*C. limbatus* (Fab.)	*D. hamata* (Boh.)	*D. fairmairei* (Perris)	*D. pellucida* (Fab.)	*M. fieberi* (Scott)	*C. nigrolineatus* (Scott)	*St. minutus* (Fab.)
No. of specimens collected	1008	386	127	156	70	125	67	13	64
No. of stylopised specimens	128	68	36	10	3	6	1	2	2
% of stylopisation	12·7	17·6	28·3	6·5	4·3	4·8	1·5	15·4	3·3
No. of adults	353	134	49	28	33	19	33	1	56
No. of stylopised adults	57	20	27	2	2	3	1	—	2
% of stylopisation in adults.	16·1	15	55	7	6	17	3	0	3·6
No. of males	161	63	21	17	12	11	15	1	21
No. of stylopised males	24	11	9	2	—	1	—	—	1
% of stylopisation in males	14·9	17·5	42·9	11·8	0	9·1	0	0	4·8
No. of females	192	71	28	11	21	8	18	—	35
No. of stylopised females	33	9	18	—	2	2	1	—	1
% of stylopisation in females	17·2	12·6	64·3	0	9·5	25	5·6	—	2·9
No. of nymphs	655	252	78	128	37	106	34	12	8
No. of stylopised nymphs	71	48	9	8	1	3	—	2	—
% of stylopisation in nymphs	10·8	19	11·5	6·3	2·7	2·8	—	17	0

Relations to the Host.

When the triungulinids leave their mother, they crawl over the body of the Delphacid and are scattered throughout the grass. Their chance of finding a host is probably greater than that of triungulinids of the genera which attack bees and wasps, for here the Delphacids live gregariously among the grasses on which they feed. Groups of different species live quite close to each other, if not mixed with one another, so it is relatively easy for the triungulinids to find them. The triungulinid adheres to the body of the host. The power of adhesion is very well developed. I pickled some Delphacids that had been

infected in the laboratory. After seven months in alcoholic-glycerine, the triungulinids were found still sticking to their bodies and could not be removed except by scraping with a needle. The Delphacids do not make any effort to get rid of the triungulinids. The parasite eventually works its way through the intersegmental membrane into the body of the host. Numbers of triungulinids were observed on the bodies of DELPHACIDAE (in the laboratory) and, in all cases, after about ten minutes they disappeared inside. When in the host's body, they either stay underneath the tergites, usually the sixth, near to the heart; or they travel to the thoracic region where they usually locate themselves near the filter chamber, where absorption of food takes place. None was found in the pleural region or in other parts of the body. They grow in a position parallel to the gut, extending from the filter chamber down into the abdomen.

The cap of the male puparium appears either on the left or right side on one of the pleura 5–8, usually between 7 and 8 on the left side.

The cephalothorax of the female appears externally only in the adult stages of Delphacids; on either side of the abdomen in one of the pleura 3–8, usually 7 on the right side.

Table X shows the number of the caps of male puparia (♂), and also the number of protruding females (♀) on the different abdominal pleura of the host.

R = on the right side of the body of the host.
L = on the left side of the body of the host.
3 = on the third pleuron. The same applies to 4, 5, 6, 7, 8.
3–4 = between the third and fourth pleuron. The same applies to 4–5, 5–6, etc.

TABLE X.

Segment	Side	♂	♀
3	R	—	1
	L	—	1
3–4	R	1	—
	L	—	—
4	R	1	1
	L	—	1
4–5	R	—	—
	L	—	—
5	R	1	5
	L	1	—
5–6	R	2	1
	L	—	—
6	R	2	6
	L	4	2
6–7	R	6	2
	L	5	—
7	R	9	16
	L	12	9
7–8	R	9	1
	L	19	2
8	R	2	—
	L	—	1

Of the nine species of DELPHACIDAE I collected, I have never found a nymph having the external cephalothorax of a female parasite. In this respect, my

observations do not agree with those of Perkins (1905 : 98), who stated that in the case of *Elenchus tenuicornis* (Kirby) the nymph or adult Delphacid would produce parasites of either sex.

In very few cases I have found a host having two parasites. Out of the 122 infected specimens that I have collected, six only have had two parasites. One has a male puparium and an adult female; the former is anterior to the latter. The cap is on the right fifth pleuron, and the cephalothorax of the female on the right sixth pleuron. Three specimens have two male puparia; in one they are on the left side; in another they are on the right side; and in the third one on the left and the other on the right side. Two specimens have two females; in one both on the right; and in the other one on the left and one on the right side.

I never found three or more parasites in any Delphacid; perhaps too heavily parasitised a host would normally die before the larvae of *Elenchus* were fully grown. Dr. O. W. Richards collected, from the Willow Field on 23 September 1932, an abnormal female of *Delphacodes pellucida* (Fab.) with a female *Elenchus* protruding from its body; when examined on the 29th, it had 3 female parasites. On the same day he collected also from the same field a Delphacid nymph with three empty male puparia in its body. It died in the evening.

It appears that *E. tenuicornis* is restricted to Delphacids and does not infect other insects in the Willow Field. Three Jassid nymphs were collected with the 350 Delphacids collected on 26 July 1935. The Jassids were exposed to triungulinids. They were pickled on the 27th; when dissected they were found to contain no triungulinid either adhering to or inside their bodies. This apparent immunity was developed although there were far fewer (27%) true hosts (DELPHACIDAE) than triungulinids, of which there were about 1475.

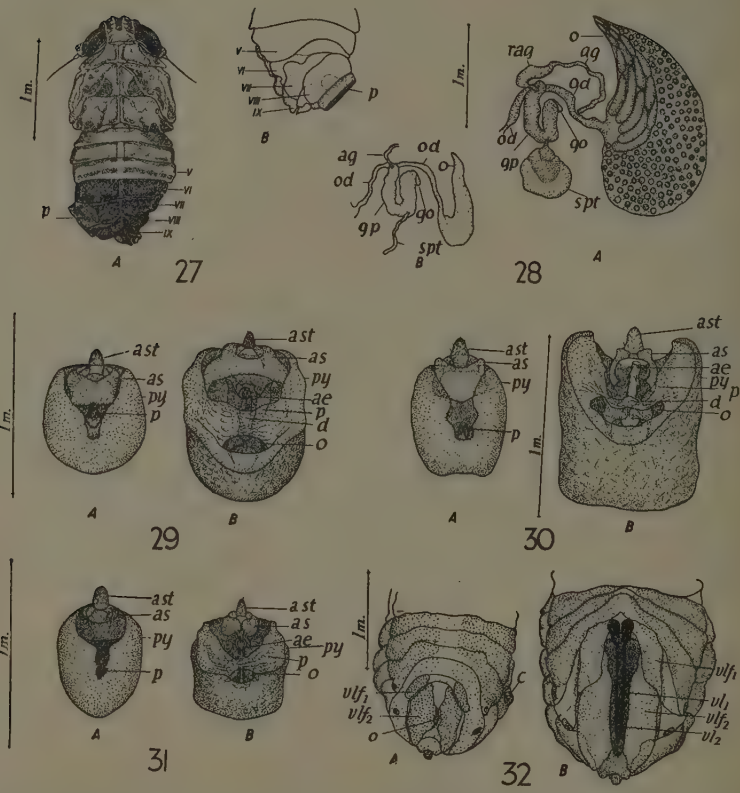
Effects of Parasitism on the Host.

a. *Reduction in powers of multiplication.*

Although the parasite lives within the host without actually destroying any of its organs, the latter is disabled by the absorption of its body fluid by the parasite.

If the Delphacid spends a long time in the nymphal stage, the parasite affects the growth of the reproductive system. As mentioned earlier, nymphs that hibernate do not reach the adult stage if they contain the larva of a male parasite; if they contain that of a female, the nymph reaches the adult stage but with a degenerate reproductive system. On dissecting specimens of *C. williamsi* China and *D. pellucida* (Fab.) (seven females in all) that contained female parasites and had reached the adult stage, I found that the female Delphacid had a normal genital pouch, but the accessory glands and spermatheca were reduced. The ovaries were also reduced and contained no eggs at all (fig. 28, B). I was not able to find any trace of gonads in nine specimens having reduced external male genitalia. On the other hand, on dissecting females of *C. limbatus* (Fab.) whose nymphs, developing rapidly (as seen in Table II, p. 353), reach the adult stage even when parasitised, I found that the ovaries contained perfectly developed eggs, though fewer than usual. Three couples of stylopised *Conomelus* were put together but in no case was any pairing observed.

Thus *Elenchus* has some effect on the number of Delphacids either by complete castration or by reduction in the number of the offspring. But as the parasitism in the Willow Field does not reach a high percentage (as seen



FIGS. 27–32.—(27) A nymph of *Criomorphus williamsi* China—Stylopised and deformed. A = Dorsal view of the whole body. B = Ventral view of the deformed part of abdomen. P = head of an empty puparium of male *Elenchus*. V to IX = the fifth to the ninth abdominal segments; (28) Internal genitalia of a female Delphacid. A = normal internal genitalia. B = reduced internal genitalia as a result of stylopisation. ag = accessory glands; go = genital opening; gp = genital pouch; o = ovary; od = oviduct; rag = reservoir of the accessory gland; spt = spermatheca. (Terminology after Snodgrass—(1933 : 98)); (29) External genitalia of male *Criomorphus williamsi* China. A = deformed external genitalia as a result of stylopisation. B = normal external genitalia. ae = aedeagus; as = anal segment; ast = anal style; d = diaphragm; o = ventral opening of pygofer; p = genital style of paramere; py = pygofer. (Terminology after Giffard—(1921 : 139)); (30) External genitalia of *Dicranotropis hamata* (Boh.). A = deformed. B = normal; (31) External genitalia of *Delphacodes pellucida* (Fab.). A = deformed. B = normal; (32) External genitalia of female *Criomorphus williamsi* China. A = deformed. B = normal. c = cephalothorax of female *Elenchus*; VI_1 and VI_2 = first and second valvulae; VIf_1 and VIf_2 = first and second valvifers; o = reduced ovipositor. (Terminology after Snodgrass (1933 : 96)).

in Table IX (p. 377)) and as it is mainly confined to certain parts of the field, the numbers of any species in the field are probably not very seriously affected. Possibly local colonies of Delphacids may sometimes be exterminated.

b. *Alteration of general features of the host.*

There are practically no alterations in the general features of a Delphacid infected with *Elenchus*. If the insect is in the nymphal stage, there is no change either in size or in colour from the normal condition. Distortion of the segments occurred in one nymph of *C. williamsi* China whose abdomen was badly distorted (fig. 27). Usually the parasite appears in the pleural region of the abdomen which is soft and easy for the parasite to penetrate without distorting any sclerites. If the host reaches the adult stage, the colour is usually modified in the male to resemble that of the female Delphacid; the female is unmodified.

The abdomen of the host usually bulges on the side pierced by the cephalothorax of the parasite. In the few cases where distortion results, both tergites and sternites are deformed at the region where protrusion takes place. Repair of the distorted part is remarkable. The cephalothorax of the male puparium or of the adult female may appear in the middle of an instar quite apart from any moulting. This shows that they do not penetrate through a hole specially made in the new cuticle; but that by their struggles within the host, they rupture the pleuron. This repairs itself very quickly and forms a ring round the protruded part of the parasite and gives it a strong hold.

c. *Alteration of external sexual characters.*

Secondary sexual characters.

The male of a Delphacid is darker in colour than the female; the markings may also be different. The male is also smaller than the female. All these secondary sexual characters appear to be changed into those of the female in any stylopised adult male Delphacid. There is no tendency for females to assume male characters. These changes have not been studied in detail.

Primary sexual characters.

In species of Delphacids that hibernate as eggs, and have a short nymphal period, the primary sexual characters are not affected at all, e.g., *C. limbatus* (Fab.). The stylopised female of this species has a normal ovipositor; even the eighth and the ninth sternites that form the armature of the female genitalia do not show any changes. Further, as already mentioned, such females may contain eggs. The male also possesses complete normal male genitalia. The testes are of normal size.

In the other species which hibernate as nymphs, and in which the triungulinids have enough time to produce an effect on the primary sexual characters, the females still nearly always have normal external genitalia, with fully developed ovipositor, sheath, and armature. In contrast to the female, no Delphacids of this type were found with normal male genitalia. Such specimens appear always to be a type of degenerate male, in which the pygofer, with the diaphragm, forms a ring around the anal segment. The only male elements represented are the parameres, though they are in a very reduced state; either separate or fused together into a small structure attached to the pygofer internally at its ventral margin (figs. 29–31). I found only one reduced female of *C. williamsi* China (fig. 32): it contained a female *Elenchus*. Its ovipositor was much reduced and represented by a small appendage at the centre of the

ninth sternite. There was no sheath around it, the eighth sternite was very much reduced, while the ninth was large. Haupt (1933 : 255) found that three males out of twelve *Delphacodes pellucida* (Fab.) collected at Bellinchen were sexually abnormal. One specimen resembled my reduced males, but the others were more normal. He did not find a cephalothorax of a Stylopid in the body and the malformation did not appear to be due to parasitic castration, nor were the specimens gynandromorphs. I have not met with such a case; all the deformed Delphacids I have seen were stylopised.

d. *Effects resulting from emergence of the male or of the triungulinids.*

The emergence of the male does not necessarily cause the direct death of the host. The host may die the next day or live for a considerable time. Table IV (p. 373) shows the length of life of different Delphacids after the emergence of the male parasite. Spores of fungi, however, sometimes grow in the empty puparium. In some cases fungus grows on the body of the host around the head of the puparium. Perkins (1905 : 93) states, "Again in the case of Leafhoppers, at least at certain seasons, no sooner does the male parasite emerge than a fungus disease at once starts its attack in the opening thus made, the results of which are absolutely deadly."

Fungus may even be fatal to male *Elenchus* in their pupal stage when the host dies. The day after the death of the host fungus was found growing on the host, and it continued its growth until it covered the insect and the male pupa did not develop. Mr. Petch identified this fungus as *Mucor mucedo*.

The emergence of the triungulinids invariably causes the death of the host. The three Delphacids from which the triungulinids emerged in the laboratory were dead the next day.

Summary.

1. The nine species of Delphacidae dealt with are *Conomelus limbatus* (Fab.) and *Delphacodes fairmairei* (Perris)—(hibernate as eggs); *Criomorphus williamsi* China, *Delphacodes pellucida* (Fab.), and *Dicranotropis hamata* (Boh.) —(hibernate as nymphs); *Criomorphus nigrolineatus* (Scott), and *Delphacodes difficilis* (Edw.)—(probably hibernate as nymphs); *Stenocranus minutus* (Fab.), and *Megamelus fieberi* (Scott)—(hibernate as adults).

2. Their life-history and the stages present at Slough at any time of the year are recorded. A key for the identification of the nymphs has been prepared.

3. Fungi of the species *Mucor mucedo*, *Cephalosporium* sp., and *Acremonium* sp.; and nymphs of mites of *Trombidium* sp. (and probably other species) live saprophytically or parasitically on Delphacids.

4. A Mymarid parasite *Anagrus incarnatus* (Haliday) of the type described by Bakkendorf (1925) as a variety with a long ovipositor, was bred from eggs of *Conomelus limbatus* (Fab.); a Dryinid parasite *Dicondylus bicolor* (Haliday) was bred from nymphs of *Dicranotropis hamata* (Boh.); and a Stylopid parasite *Elenchus tenuicornis* (Kirby) was bred from all the species except *Delphacodes difficilis* (Edw.).

5. The description as distinct species of specimens of *Elenchus* bred from different Delphacid hosts without finding any other difference between the parasites is shown to be of doubtful value.

6. The life-history of *Elenchus* has been worked out. Descriptions of the egg, triungulinid, scarabaeidoid larva, apodous larva, prepupa and pupa of

the male; the adult male and the female are given. The scarabaeidoid and later larval stages are described for the first time. It is shown that *Elenchus* has two generations a year.

7. *Elenchus* does not attack a high percentage of the DELPHACIDAE. The effects of the parasite on the host lead to a reduction in powers of multiplication either by the degeneration of the gonads or by reducing the number of eggs formed in the ovaries; to the change of the secondary sexual characters of the male into those of the female (those of the female do not change); and to the reduction of the external male genitalia (there are very few examples of female hosts with reduced genitalia). The emergence of males and triungulinids leads after a time to the death of the host.

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